THE UNIVERSITY OF ALBERTA

SPRUCE-FIR FORESTS OF THE HIGHLANDS OF NORTHERN ALBERTA

by

© PETER L. ACHUFF

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA
SPRING, 1974

ABSTRACT

Thirty stands of spruce-fir forest in highland areas of northern Alberta were studied. The highlands are cooler and receive more precipitation than the adjacent lowlands during May - September. Orthic Grey Luvisols were the most common soil type.

Based on a morphological index evaluation the spruce was basically Picea glauca and the fir Abies balsamea. The pine was nearly all Pinus contorta var. latifolia. A Geographic Index, based on the spruce, fir and pine species, showed increasing "boreality" from west to east and high to low altitude.

Four community types were recognized using a Bray-Curtis ordination with Sørenson's coefficient of community based on cover data: Rubus pedatus/Ptilium, Cornus-Linnaea, Viburnum/Hylocomium, Calamagrostis canadensis. The community types were related to trends of altitude, soil nutrient status, and two groups of correlated vegetational variables.

The floristic and vegetational affinities of the community types with adjacent regions are discussed.

The spruce-fir forests studied are considered to be a climax vegetation type with balsam fir dominance indicated at higher altitudes, shifting to white spruce dominance at lower altitudes.

ACKNOWLEDGEMENTS

I wish to thank Dr. George H. La Roi for his advice and encouragement during the course of this thesis; the members of my advisory committee for their aid; the Department of Soil Science, University of Alberta and the Research Branch, Canada Department of Agriculture for the use of laboratory equipment; Tim Achuff for his help as a field assistant for two summers; and the following taxonomists for identifying or confirming the identity of voucher specimens: D.M. Britton, M. Dumais, M. Ostafichuk, W. Peterson, D.H. Vitt.

Special appreciation is due my wife, Elsie, for her support in the field, the laboratory, and at the typewriter.

Financial support was received from the Department of Botany, University of Alberta; the Boreal Institute for Northern Studies, (Grant-in-aid 1971-1973); and the National Research Council of Canada (Operating Grant No. A-2750 La Roi).

ACKNOWLEDGEMENTS

I wish to thank Dr. George H. La Roi for his advice and encouragement during the course of this study; the members of my advisory committee for their aid; the Department of Plant Science, University of Alberta and the [illegible] Branch, [illegible] Department of Agriculture for the use of laboratory equipment; [illegible] for her help as a field assistant for two summers; and [illegible] the following taxonomists for identifying or confirming the identity of certain specimens: [illegible], [illegible], [illegible], [illegible], [illegible], [illegible].

Special appreciation is due to [illegible] for her patience in the thesis, the laboratory, and at the typewriter.

Financial support was received from the Department of Botany, University of Alberta; the Boreal Institute for Northern Studies, (Grant-in-aid [illegible]) and the National Research Council of Canada Operating Grant No. A-[illegible] to Dr. La Roi.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

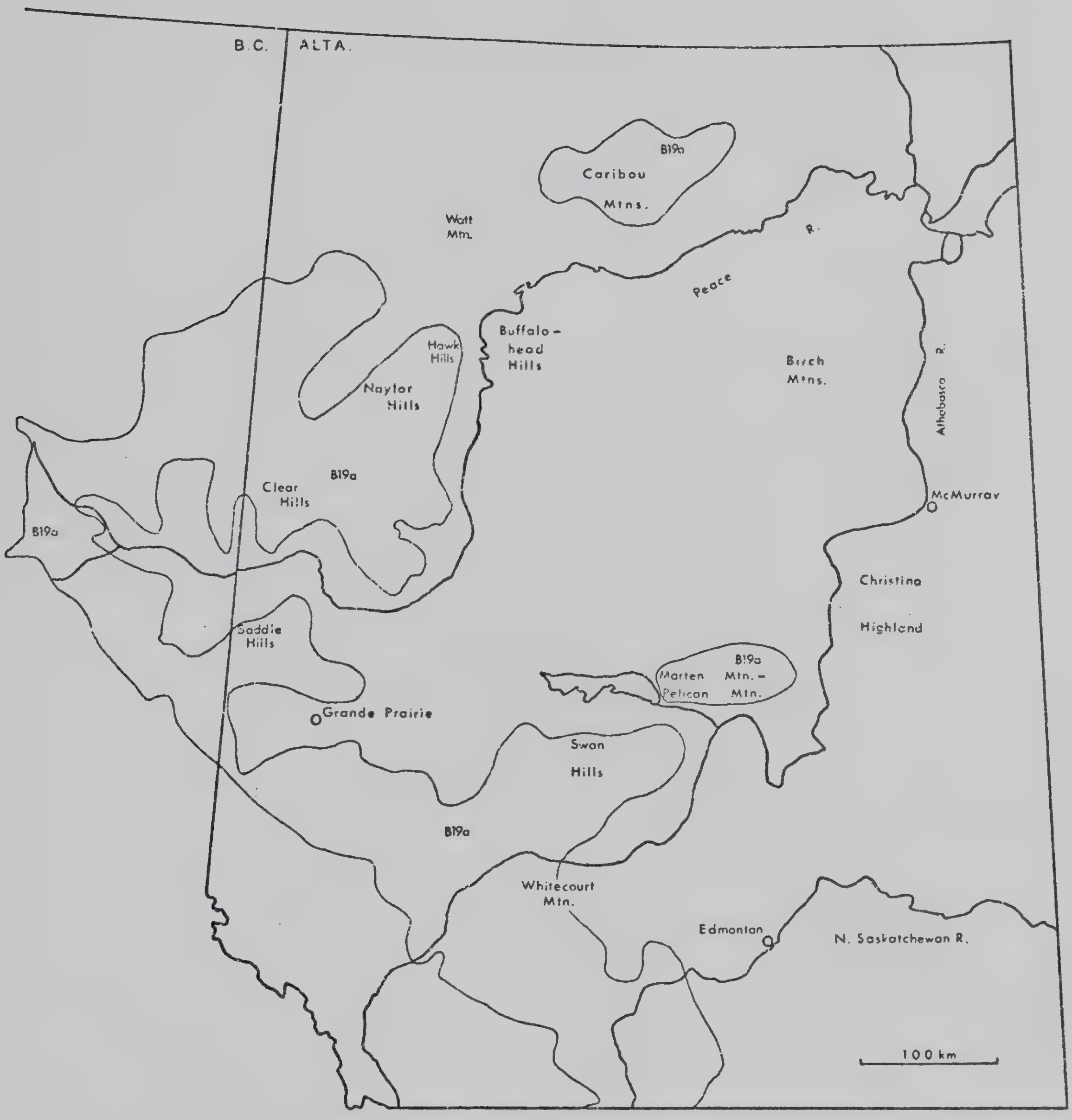
INTRODUCTION

The Lower Foothills Section (B19a) of Rowe's (1959) classification of the forests of Canada, is transitional between the Boreal and Subalpine Regions. The section covers much of the eastern slope of the Rocky Mountains in Alberta and British Columbia (Figure 1). Isolated eastern and northern outliers of the section occur on highland plateaus, usually surrounded by the Mixedwood Section (B18a) at lower elevations.

During the summers of 1971 and 1972, the spruce-fir forests of ten highland areas in northern Alberta were investigated (Figure 2).

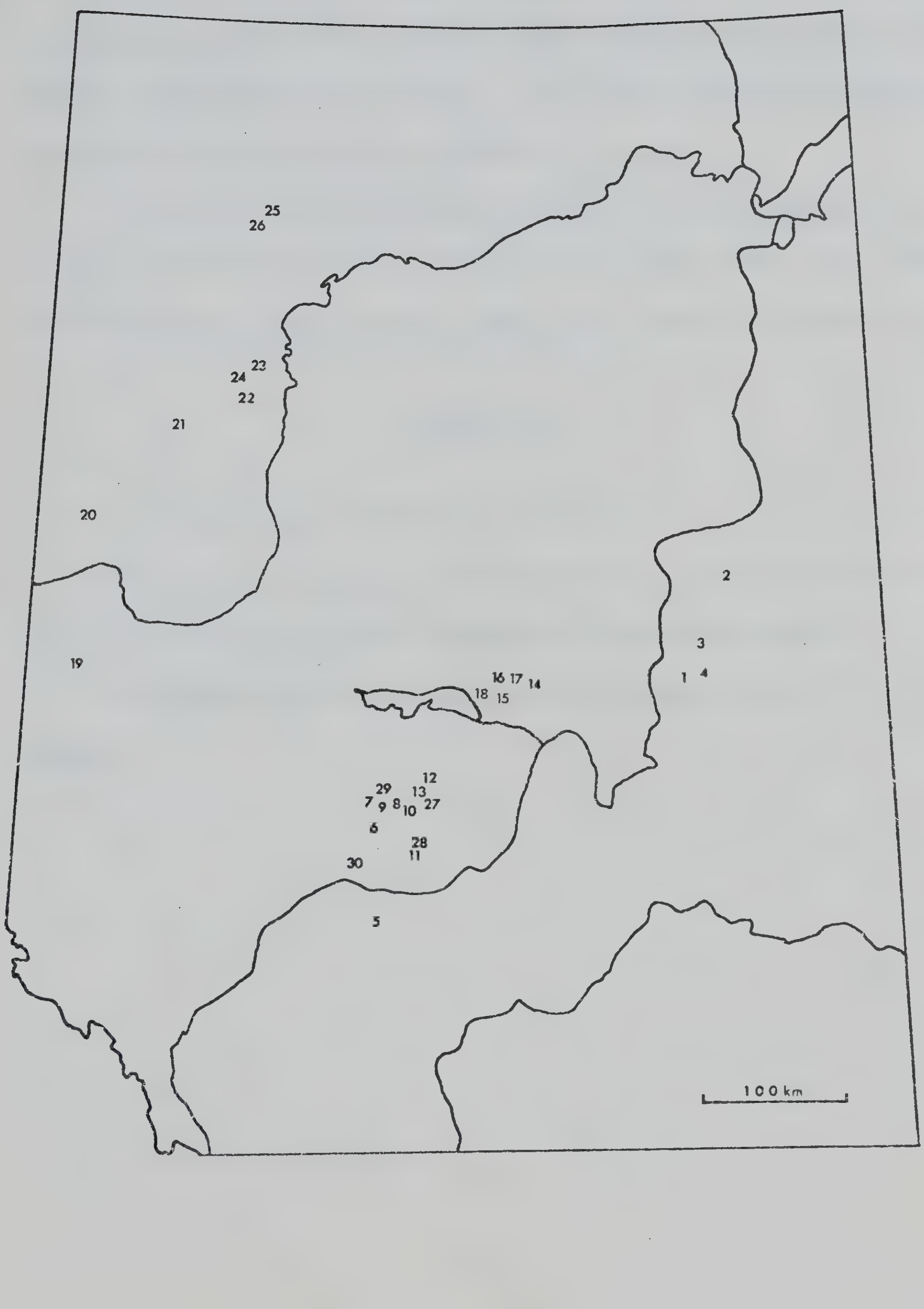
Upland sites in the study area are forested except where fires have created seral non-forest communities dominated by shrubs and tree regeneration. Fires are frequent in the boreal forest and old-age forests dominated by spruce and/or fir, such as those studied here, are relatively rare. The rarity of such forests is being increased by the harvesting of such "overmature" stands under the management plans of the Alberta Forest Service. At the present time there are no old-age spruce-fir forests in the study area with any kind of conservation protection. Several of the stands studied during the summer of 1971 have since been harvested. Since old-age forests cover the smallest area of any forest type in northern Alberta, the protection of examples of them for scientific research and educational purposes should be given high priority.

Figure 1. Location of study area.



B.C.
ALTA.
B19a
Caribou
Mtns.
Watt
Mtn.
R.
Peace
Buffalo-
head
Hills
Hawk
Hills
Naylor
Hills
Birch
Mtns.
Athabasca R.
B19a
Clear
Hills
McMurray
B19a
Christina
Highland
Saddie
Hills
B19a
Marten Mtn. -
Pelican Mtn.
Grande Prairie
Swan
Hills
B19a
Whitecourt
Mtn.
Edmonton
N. Saskatchewan R.
100 km

Figure 2. Location of stands.


25
26
23
24
22
21
20
19
2
3
1
4
16
17
14
18
15
12
29
13
7
9
8
10
27
6
28
11
30
5
100 km

The bulk of the upland forest is composed of seral aspen, aspen-spruce, or spruce-aspen forest at lower altitudes (generally below 1000m), while at higher altitudes lodgepole pine replaces aspen as the main seral species, thus resulting in seral pine, pine-spruce, and spruce-pine forests. At lower elevations on sandy soils jack pine forests are not uncommon.

Previous descriptions of portions of these forests can be found in the works of Raup (1933, 1934, 1946), Moss (1953, 1955), Moss and Pegg (1963), La Roi (1964), and Lesko and Lindsay (1973).

OBJECTIVES

The objectives of the research were:

1. a phytosociological description and classification of mature spruce-fir forests in the highlands of northern Alberta.

2. a description of selected site characteristics within each stand.

METHODS

Floristic Methods

Voucher specimens were collected from all stands and deposited in the University of Alberta Herbarium (ALTA). Nomenclature follows Moss (1959) for vascular plants, with the exceptions of Dryopteris (Britton 1972) and Betula (Dugle 1966); Lawton (1971) for mosses; Schofield (1968) for hepatics; and Hale and Culberson (1970) for lichens.

Cones and branches of Picea glauca (white spruce), P. engelmannii (Engelmann spruce), Abies balsamea (balsam fir), A. lasiocarpa (subalpine fir), Pinus banksiana (jack pine) and P. contorta var. latifolia (lodgepole pine) were collected randomly in each stand in which they occurred.

The spruce collections were evaluated with a morphological index (Table 1) based on earlier work by Garman (1957), Horton (1959), Taylor (1959), La Roi and Dugle (1968), and Roche (1969). The criteria of the earlier workers were evaluated by examining material collected outside the area of suspected hybridization in Alberta and adjacent areas of Saskatchewan, British Columbia, and Montana. The scale apex criteria in Table 1 were taken from Horton (1959) and Taylor (1959). All other criteria in Table 1 were taken from La Roi and Dugle (1968) after Garman (1957). The diagrams of cones and cone scales of Horton (1959) and Roche (1969) were also consulted.

Table 1. Spruce Morphological Index Criteria. _Picea glauca_ = 1
Intermediate = 2
P. engelmannii = 3

Branchlet pubescence	glabrous	1
	slightly pubescent	2
	pubescent	3
Cone length	<4.4 cm	1
	4.4 - 5.3 cm	2
	>5.3 cm	3
Scale length	<1.17 cm	1
	1.17 - 1.40 cm	2
	>1.40 cm	3
Scale length/width ratio	<1.43 cm	1
	1.43 - 1.52 cm	2
	>1.52 cm	3
Scale shape	obovate triangular	1
	intermediate	2
	elliptic	3
Scale texture	stiff	1
	intermediate	2
	flexible	3
Scale margin	entire	1
	wavy	2
	erose	3
Scale apex	broadly rounded	1
	intermediate	2
	narrow and wedge shaped	3
Bract shape	spatulate	1
	intermediate	2
	lanceolate	3
Bract apex margin	finely toothed	1
	intermediate	2
	erose	3
Bract length/scale length	<0.37 cm	1
	0.37 - 0.42 cm	2
	>0.42 cm	3

A general problem in the use and interpretation of morphological indices is that of character independence, i.e. the weighting of a character by measuring it several different ways. Weighting may also be due to genetic linkage between characters. For example, is the criterion of scale length independent of scale length/width ratio, or has the same character been measured and used twice? Present knowledge of the inheritance of characters in the species examined here is insufficient to resolve this matter.

A second problem is the use of qualitative or semi-quantitative, intergrading characters and the setting of character state limits. For example, in the criterion scale shape how does one draw the line between the character states obovate-triangular, intermediate, and elliptic in a consistent, reproducible manner? In this study a preliminary examination of the collections was made to familiarize the writer with the range of variation. Then, using the descriptions and diagrams of earlier workers and reference collections from non-hybridized populations, character state limits were formulated. By repeated reference to descriptions, diagrams, and reference collections during the evaluation of the suspected hybrid collections, it is felt that the morphological index criteria were applied in an objective, reproducible manner.

The index value for each cone and branch collection was calculated as the mean of the 11 criteria values, thus having a possible range of one to three. Twenty-five cones and branches from each stand were examined. The stand morphological index value was cal-

culated as the mean of the 25 individual cone and branch collections; again, having a possible range of one to three.

Morphological characters for evaluating the fir collections were difficult to find. This difficulty is indicative of both the close relationship of the two species, and that the genus is "genetically conservative" (La Roi and Dugle 1968), such that morphological differences within the genus as a whole are small. The characters used (Table 2) were chosen primarily on the basis of the taxonomic descriptions of Moss (1959). Other works consulted were Harlow and Harrar (1958), Preston (1961), and Bakuzis and Hansen (1965). The characters used by these workers were evaluated using herbarium specimens of balsam fir from east-central Alberta (Cold Lake), Manitoba, Ontario, Quebec, and New Brunswick, and subalpine fir from south-western Alberta (Waterton Lakes N.P.), Montana, and southern British Columbia.

The problems of character weighting and character state limits discussed above, in regard to spruce, apply here as well. The problem of character weighting is presently insolvable and the character state limits were chosen in an analagous way as for spruce.

The index value for each cone and needle collection was calculated as the mean of the three criteria values, thus having a possible range of one to three. Ten cone and needle collections from each stand were examined. The stand morphological index value was calculated as the mean of the ten individual cone and needle collections; again, having a possible range of one to three.

Table 2. Fir Morphological Index Criteria: Abies balsamea = 1
Intermediate = 2
A. lasiocarpa = 3

Scale width	<1.5 cm	1
	1.5 - 2.0 cm	2
	>2.0 cm	3
Scale length/bract length	<2	1
	2 - 3	2
	>3	3
Stomatal band position	below only	1
	intermediate [a]	2
	above and below [b]	3

[a] stomatal band running <3/4 length of the upper side of the needle

[b] stomatal band running >3/4 length of the upper side of the needle

Table 3. Morphological features used in pine identification (Moss 1949). P.c. = Pinus contorta var. latifolia, P.b. = P. banksiana.

Branch habit:	P.c. - ends usually curve upward
	P.b. - ends usually droop
Bark:	P.c. - darker, small scales
	P.b. - irregular, scaly ridges and furrows
Cone shape:	P.c. - ovoid or conical
	P.b. - strongly incurved
Cone scale	P.c. - umbonate with long, recurved prickle
	P.b. - unarmed or with minute prickle
Cone Orientation:	P.c. - directed toward branch base or perpendicular
	P.b. - directed toward branch tip

Pine occurred in the study stands with a very low density and thus a morphological index approach was not used. Rather, the trees in each stand were rated as *Pinus contorta*, Intermediate, or *P. banksiana*, and the stand was then rated as consisting wholly or predominantly of a certain type. The criteria used (Table 3) were those of Moss (1949).

Selection of stands

A preliminary selection of stands was made using forest cover maps (1:126,720) and aerial photographs (1:31,680). The selected stands were then checked on the ground, using the following criteria:

1) at least three hectares in area

2) dominated by one or any combination of *Picea glauca*, *P. engelmannii*, *Abies balsamea*, or *A. lasiocarpa*

3) reasonably uniform in topography, slope and aspect

4) not in an alluvial flat, bog, or ravine

5) not recently disturbed by man, fire, or other natural disturbance

6)if *Picea glauca* or *P. engelmannii* present, some trees at least 30.5 cm dbh (diameter at breast height = 1.35 m) or some trees of other species at least 23.0 cm dbh.

Thirty stands were located and sampled (Figure 2).

Vegetation Sampling

A restricted random sampling technique was used. A baseline was laid out through the stand. The center of each set of nested quadrats was located by pacing a random distance along the baseline

and then pacing a second random distance perpendicular to the baseline. If the second random number was even, the set was to the left of the baseline; if odd, to the right. Maximum and minimum random distances were 50 m and 10 m respectively.

The vegetation was divided into four layers: the tree layer (woody plants >7.5 cm dbh), the shrub layer (woody plants <7.5 cm dbh and >30 cm tall), the herb-dwarf shrub layer (all herbs regardless of height, woody plants <30 cm tall), and the bryoid layer (terrestrial bryophytes and lichens).

Cover was estimated by the canopy coverage method of Daubenmire (1959). "Canopy coverage is defined as the percentage of the ground surface included in the vertical projection of a polygon drawn about the extremities of the undisturbed foliage of a plant" (Daubenmire 1970). Cover estimates were made for each species using six cover classes: 1 (<1 - 5%), 2 (6 - 25%), 3 (26 - 50%), 4 (51 - 75%), 5 (76 - 95%, 6 (96 - 100%). Cover class midpoints were used in computing means. Total cover per layer was computed as the sum of the mean cover values of the component species and thus sometimes exceeded 100%.

A 10 X 10 m quadrat was used to sample the tree layer. Sampling trials showed that 20 quadrats per stand would result in a standard error of <10% of the mean density per quadrat of all trees, and a standard error of <15% of the mean density per quadrat of the most common tree species. In each quadrat cover, density and dbh (living and dead) were measured. Basal area was later computed using the dbh's.

A centrally nested 5 X 5 m quadrat was used to sample the shrub layer. The adequacy of 20 quadrats per stand was evaluated with a species-area graph, plotting cumulative number of species against cumulative number of quadrats. Arithmetic, equivalent-scale axes were used. In the four trial stands the curve had flattened out by 15 quadrats, and in most cases, no new species were added after ten quadrats. In each quadrat cover was estimated for all species and density was measured for tree saplings (<7.5 cm dbh and >1 m tall) and transgressives (between 30 and 100 cm tall).

A centrally nested 1 X 1 m quadrat was used to sample the herb-dwarf shrub layer. The adequacy of 20 quadrats per stand was evaluated as for the shrub layer. Twenty quadrats appeared sufficient in some stands but not in others. However, when the number of species sampled at 20 quadrats was compared with the estimated total stand herb-dwarf shrub flora, it was found that nearly the entire flora had been recorded and that all the species contributing significant amounts of cover had been sampled. The total flora of each stand was estimated by collecting plants throughout the stand, whether they occurred within the quadrats or not. Cover was estimated for all species, and density was measured for tree seedlings (<30 cm tall) in each quadrat.

The bryoid layer was sampled with five 20 X 50 cm quadrats placed randomly within the 1 X 1 m herb-dwarf shrub quadrat. Due to identification difficulties during the sampling trials, a species-area curve was not used. The method was judged adequate because the

species contributing major amounts of cover were all sampled. Subsequent species-area curves show the method to be acceptable.

Epiphytic lichens and mosses were collected in each stand, but no quantitative estimate of their abundance was made.

Ten to fifteen increment cores were taken at breast height in each stand. Trees from various size classes were included to assess the date of stand establishment and stand age structure. Stand Age was computed as the mean age at breast height of the five oldest trees cored. The height of the cored trees was measured with a Haga altimeter. In eight stands, fifteen to twenty saplings, transgressives, and seedlings were each cut at the base for age determinations.

Growth rate calculations for white spruce and balsam fir were based on diameter rather than the more commonly used height. Height is generally considered to be indicative primarily of site quality, while diameter is influenced more by density (Baker 1950). Thus, the growth rate curves reflect both site quality and stand history, primarily density. Diameter was used because many more tree diameter measurements were available for each stand than height measurements.

Linear regression lines, using dbh as the independent variable and age as the dependent variable, were used to compare the diameter growth rates of white spruce and balsam fir among the community types. The regression lines were later used to predict age from dbh in the construction of age structure curves for each stand.

Soils

A main soil pit was dug in a central part of each stand. A brief profile description and sampling of the B and C horizons were done in the main pit. Composite samples of the L-H and A horizons were drawn from the main pit and several shallow pits located throughout the stand. The samples were dried in the field and stored air-dry for later analysis. All samples were ground and the portion passing a 2 mm sieve was used for subsequent analyses. The samples were analyzed for color (Munsell color chart); texture (Bouyoucos 1951, modified by shaking for one hour in a reciprocal shaker); % available soil water (1/3 bar % - 15 bar %, ceramic plate extraction); total exchange capacity (sodium chloride extract distilled into boric acid and titrated with sulfuric acid); Na^{+}, K^{+}, Ca^{++}, Mg^{++} (ammonium acetate extraction, atomic absorption spectrophotometer); pH (soil paste-glass electrode); and free lime (dilute HCl). Horizon, drainage class, and soil classification nomenclature follow The System of Soil Classification for Canada (Canada Department of Agriculture 1970).

Ordination

The stands were ordinated using the Bray and Curtis (1957) technique, Beal's (1960) equations for axis distances, and Sørenson's (1948) coefficient of community (Easton and Precht no date). Gauch and Whittaker (1972), in comparing several ordination techniques and similarity measures, have concluded that the above combination is generally best. Ordinations were done based both

on mean cover values and on Prominence Values. The Prominence Value used here was modified from Beals (1960) by La Roi (1964, p. 284): Prominence Value = (mean cover %)($\sqrt{\text{\% frequency}}$).

Cluster Analysis

Cluster analysis, a polythetic, agglomerative, hierarchical technique (Pritchard and Anderson 1971), was performed using Prominence Values and cover values (Conway 1972). The following techniques of cluster formation were used: nearest neighbor, furthest neighbor, group average, centroid clustering, minimum variance.

STUDY AREA

Climate

The climate of northern Alberta is continental with cold winters and short, cool summers. Precipitation reaches a peak in early July and is lowest approximately six months later in mid-winter (Sabbagh and Bryson 1962). July is the warmest month, while January is the coldest.

Climatic data for the highlands are available only for May through September, which generally is the growing season. Table 4 compares the May - September climatic data of the highland stations with adjacent lowland stations. The data are for a minimum of ten years' record (1962 - 1971). All paired data are for comparable periods.

Total May - September precipitation is from 2.5 to 16.5 cm higher for the highland stations, apparently due to localized orographic effects (Muttit 1961, MacIver 1970). Likewise, the mean May - September temperature of the highland stations is from 0.1° to 3.0° C cooler.

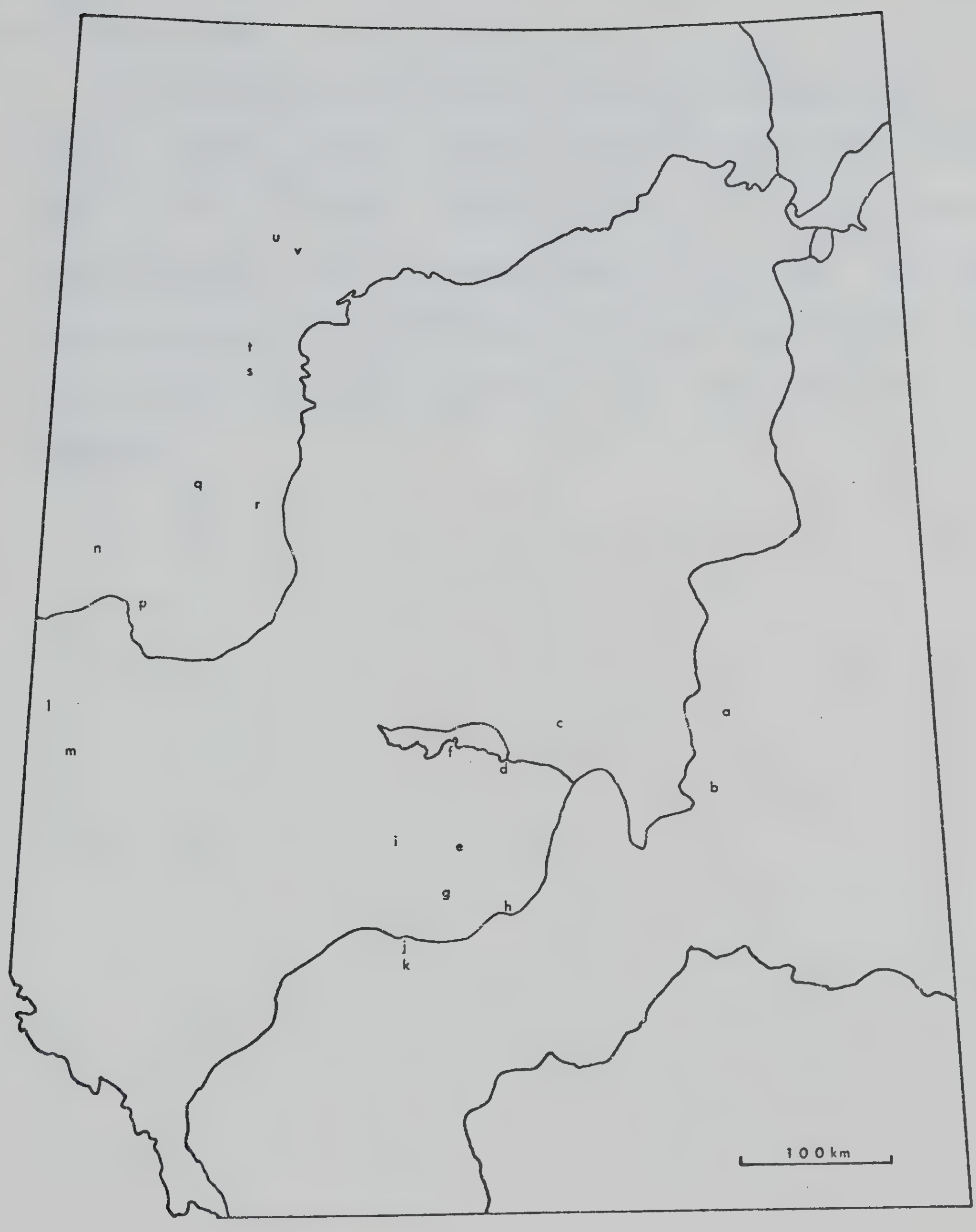
Geology and Physiography

The highlands are erosional remnants underlain by sandstones and shales of late Cretaceous or Tertiary age (Bayrock 1959, 1960, 1963; Green and Mellon 1962; Jones 1962, 1966; Reeder and Odynsky 1969; Wynnyk *et al*. 1969). The bedrock is generally flat-lying, and has been dissected to form concordant, flat-topped plateaus which rise 300 - 600 m above the rolling lowlands to altitudes of 650 - 1300 m.

Table 4. Mean temperature and total precipitation, May - September, for highland and lowland stations. (Department of Transport, Meteorological Branch). See Figure 3 for location.

Station	Altitude (m)	Mean Temp. (°C)	Total Ppt. (cm)
a. May Tower	853	11.3	43.8
b. Wandering River	594	12.7	32.8
c. Meridian Tower	930	10.8	38.9
d. Slave Lake	590	11.9	29.7
e. Swan Dive Tower	1270	10.9	40.6
f. Kinuso	595	11.7	24.1
g. Pimple Tower	1100	10.9	35.6
h. Fort Assiniboine	640	12.6	32.5
i. Goose Mtn. Tower	1340	9.0	49.3
j. Whitecourt	701	12.0	35.3
k. Whitecourt Tower	1143	9.5	38.0
j. Whitecourt	701	12.0	35.3
l. Saddle Hills Tower	1085	11.4	33.8
m. Beaverlodge	762	12.3	27.4
n. Clear Hills Tower	1067	10.5	26.9
p. Hines Creek	655	11.6	24.4
q. Chinchaga Tower	853	11.0	30.5
r. Manning	460	13.2	23.9
s. Naylor Hills Tower	732	12.1	32.0
t. Keg River	427	12.2	23.9
u. Watt Mtn. Tower	762	10.6	32.5
v. Footner Lake	324	12.0	23.1

Figure 3. Location of climatic stations used in Table 4.
See Table 4 for key to symbols.


u
v
t
s
q
r
n
p
l
m
c
a
f
d
b
i
e
g
h
j
k
100 km

On Marten Mountain and portions of Swan Hills and Clear Hills, the bedrock is capped with unconsolidated gravels of upper Tertiary age (Jones 1962).

The entire area was glaciated from the northeast by the Keewatin ice sheet during the Wisconsin maximum more than 31,000 years ago (Bayrock 1963). During glacial retreat, large, short-lived proglacial lakes were formed along the ice front. The area became available for plants about 11,000 years ago (Gravenor and Bayrock 1961). Surficial deposits of till cover much of the highlands.

RESULTS AND DISCUSSION

Soils

Soil surveys in the study area have been either Exploratory (Lindsay *et al*. 1958, 1959, 1960, 1963, 1964; Wynnyk *et al*. 1964), with classification to the subgroup level, or Reconnaissance (Odynsky *et al*. 1961; Reeder and Odynsky 1965, 1969; Scheelar and Odynsky 1968; Wynnyk *et al*. 1969) with classification to the series level. The soils of the 30 stands were classified only to the subgroup level, but reference to published series descriptions will be made where appropriate.

The parent materials of the soils consisted of till, lacustro-till, and Tertiary gravels or bedrock (Table 5). Lacustro-till occurs where till has been mixed with lacustrine deposits (Reeder and Odynsky 1969). Texturally the parent materials were generally clays to clay-loams. The pH's were generally very strongly acid (4.5 - 5.0). Soil analysis data are shown in Appendix I.

The soils of 20 stands were Orthic Grey Luvisols. They occurred on all types of parent materials on well to moderately well drained sites. Orthic Grey Luvisols appear to be the most extensive highland soil type in upland sites under spruce-fir forest vegetation. The following is a description of an Orthic Grey Luvisol from Stand 28:

Table 5. Stand physiography and soils. Parent Material: T (till), L-T (lacustro-till), R (residual Tertiary); Drainage: R (rapid), W (well), MW (moderately well), I (imperfect); Soil Type: OR (Orthic Regosol), ODB (Orthic Dystric Brunisol), DDB (Degraded Dystric Brunisol), OGL (Orthic Grey Luvisol), GGL (Gleyed Grey Luvisol), BH-FP (Bisequa Humo-Ferric Podzol).

Stand	Altitude (m)	Slope Angle (%)	Aspect (°)	Parent Material	Drainage Class	Soil Type
1	853	10	240	T	MW	OGL
2	579	0	-	T	MW	OGL
3	640	5	150	T	W	OGL
4	869	5	250	T	W	OGL
5	1113	5	5	T-R	W	OGL
6	1219	0	-	T-R	MW	OGL
7	1280	5	170	R	MW	OGL
8	1295	10	360	R	W	ODB
9	1295	5	360	R	W	DDB
10	1280	15	180	R	W	BH-FP
11	1082	0	-	T-R	MW	OGL
12	853	5	315	T	MW	OGL
13	884	10	270	T	W	ODB
14	853	5	280	T	W	OGL
15	899	15	225	T	MW	OGL
16	762	10	340	T	W	OGL
17	686	0	-	T	MW	OGL
18	975	20	360	T-R	MW	OGL
19	899	5	180	T	MW	OGL
20	1067	5	90	R	R	OR
21	808	5	160	T	W	OGL
22	777	10	90	L-T	I	GGL
23	610	5	270	T	W	OGL
24	671	10	90	L-T	MW	DDB
25	716	10	30	T-R	W	OGL
26	488	0	-	T	MW	OGL
27	1219	20	360	T-R	W	ODB
28	1112	0	-	T	W	OGL
29	1265	5	180	R	W	BH-FP
30	945	5	145	L-T	I	GGL

Horizon	Thickness (cm)	Description
L-H	5	Dark brown (10YR 3/3 moist) coniferous needle and understory leaf litter, pH 4.2.
Ae	10	Dull yellow orange (10YR 7/2 moist) loam, weak fine platy, very friable, pH 4.0.
AB	7	----------
Bt	35	Greyish yellow brown (10YR 6/2 moist) clay loam, subangular blocky, firm, pH 4.4.
BC	10	----------
C	at 67	Olive brown (2.5Y 4/3 moist) clay, glacial till, pH 4.7.

The soils in Stands 5, 6, 11, and 28 in the Whitecourt-Swan Hills area are referable to the Hubalta Series (Wynnyk et al. 1969), which is developed on non-calcareous till often underlain by the Paskapoo Formation. The soil described from Stand 7 corresponds closely to the Pegasus Series (Wynnyk et al. 1969), which is developed on fine textured material derived from the Paskapoo Formation. Stand 19 was on a Braeburn Series soil (Odynsky et al. 1961) developed on glacial till. Stand 23 was on a Dixonville Series soil (Reeder and Odynsky 1969) which was developed on acidic glacial till.

Gleyed Grey Luvisols were found in two stands on imperfectly drained sites. In both cases the parent materials were lacustro-till, neutral in reaction, and clay to clay-loam in texture. Both soils were a locally occurring, gleyed phase of an Orthic Grey Luvisol. The poorer drainage in both sites appeared to reduce the frequency and severity of fire, for the adjacent better drained areas appeared to

have burned more recently. A description of the soil in Stand 22 follows:

Horizon	Thickness (cm)	Description
L-H	8	Dark brown (10YR 3/3 moist) coniferous needle and deciduous leaf litter, pH 5.8.
Aegj	10	Grayish yellow brown (10YR 6/2 moist) loam, platy, friable with dull yellowish brown (10YR 5/4 moist) mottles, pH 5.4.
ABgj	6	-----------
Btgj	25	Brownish grey (10YR 5/1 moist) clay loam, subangular blocky firm with dull yellowish brown 10YR 5/4 moist) mottles, pH 7.1
BCg	10	-----------
Ck	at 59	Dull yellowish brown (10YR 4/3 moist) clay loam, some limestone rock fragments, pH 7.2.

Dystric Brunisols occurred in five stands. Three profiles were Orthic Dystric Brunisols, while two were classified as Degraded Dystric Brunisols. Brunisols occurred on all types of parent material, on well to moderately well drained sites. Those developed on fine textured parent materials are similar to the Boundary Complex (Scheelar and Odynsky 1968) which is an undifferentiated group of podzolics. An Orthic Dystric Brunisol from Stand 13, which was developed on till, is described below:

Horizon	Thickness (cm)	Description
L-H	4	Brownish black (10YR 2/3 moist) coniferous needle and deciduous leaf litter, pH 5.1.
Ah	4	Brownish black (10YR 3/2 moist) loam, granular, friable, pH 4.9.
Bm	30	Dull yellow orange (10YR 6/3 moist) sandy loam, weak granular, friable, pH 5.1.
BC	5	----------
C	at 43	Olive brown (2.5Y 4/3 moist) clay loam, glacial till, pH 4.0.

The following is a description of a Degraded Dystric Brunisol from Stand 9 which was developed on residual Tertiary gravels:

Horizon	Thickness (cm)	Description
L-H	8	Dark brown (10YR 3/3 moist) coniferous needle and understory leaf litter, pH 3.6.
Ae	10	Dull yellow orange (10YR 7/2 moist), silty loam, platy, friable; quartzitic cobbles (5-10 cm diameter) comprising 20-30% of volume, pH 4.7.
Btfj	25	Dull yellow orange (10YR 6/4 moist), loam, subangular blocky, firm, quartzitic cobbles (5-10 cm diameter) comprising 20% of volume, pH 4.6.
BC	5	----------
C	at 48	Dull yellow (2.5Y 6/4 moist), silty clay, residual Tertiary gravels, quartzitic cobbles (5-10 cm diameter) comprising 20-30% of volume, pH 4.7.

Bisequa Humo-Ferric Podzols were found in two stands in Swan Hills. These soils were developed on residual Tertiary deposits of the Paskapoo Formation on well drained sites. They are also similar to the Boundary Complex. The profile from Stand 10 is described below:

Horizon	Thickness (cm)	Description
L-H	10	Dark brown (10YR 3/3 moist), coniferous needle and understory leaf litter, pH 3.6.
Ae	20	Dull yellow orange (10YR 7/2 moist), silty loam, platy, friable, quartzitic cobbles comprising 10% of volume, pH 3.4.
Bf	18	Bright yellowish brown (10YR 6/6 moist), clay loam, subangular blocky, firm, quartzitic cobbles comprising 20-30% of volume, pH 4.5.
Bt	25	Dull yellow (2.5Y 6/4 moist), clay loam, subangular blocky, firm, quartzitic cobbles comprising 20-30% of volume, pH 4.4.
BC	10	----------
IIC	at 78	Pale yellow (2.5Y 8/3 moist) sandy loam, granular, friable, quartzitic cobbles comprising 60-80% of volume, pH 4.9.

An Orthic Regosol was found in one stand. The profile from Stand 20 was developed on a rapidly drained, unconsolidated Tertiary gravel deposit and is described below:

Horizon	Thickness (cm)	Description
L-H	5	Brown (10YR 4/4 moist) coniferous needle and deciduous leaf litter, pH 4.6.
Ah	6	Dull yellow orange (10YR 7/2 moist), sandy loam, granular, friable, quartzitic cobbles (8-15 cm diameter) comprising 30-40% of volume, pH 4.6.
AC	3	----------
C	at 14	Dull yellow orange (10YR 6/3 moist) clay, massive, cobbles comprising 60-80% of volume, pH 4.6.

Major Tree Species

Introgressive hybridization (Anderson 1949) between boreal and cordilleran vicariants has been reported for *Picea glauca*-*Picea engelmannii*, *Abies balsamea*-*A. lasiocarpa*, and *Pinus banksiana*-*P. contorta* in the study area (Moss 1959 *inter alia*).

Spruce

One of the earliest workers to notice the intergradation between white and Engelmann spruce was Asa Gray (Daubenmire 1968) who noted in 1878 that ". . . on its northeastern limits, between the Peace River plateau and the Athabasca, east of the Rocky Mountains, in latitude 54° and 55°, *P. engelmannii* seems to pass into *P. alba* [*P. glauca*]."

Since then, numerous workers have reported apparent hybridization between the two species at intermediate altitudes in the foothills and the mountains of Alberta, British Columbia, and Montana (Little 1953, Moss 1955, Wright 1955, Garman 1957, Horton 1959, Taylor 1959, Habeck 1965, Weaver 1965, La Roi and Dugle 1968, Ogilvie and von Rudloff 1968, Habeck and Weaver 1969).

Taylor (1959) has treated the two taxa as subspecies of *Picea glauca*. In an essentially identical proposal, Boivin (1967) has recognized the two taxa as varieties of *P. glauca*. While these proposals seem logical in view of the large amount of evidence of gene flow between the two taxa, the weight of custom has so far been against it, preferring to regard the taxa as two species in which hybridization is occurring in a limited portion of their geographic ranges.

In the Intermountain Region of the United States Picea engelmannii intergrades with P. pungens (Cronquist, et al. 1973). Daubenmire (1968) and Roche (1969) have reported hybridization between P. glauca and P. sitchensis in the Skeena River area of British Columbia. In addition, Wright (1955) has reported artificial hybridization between P. engelmannii and P. sitchensis. Thus the possibility arises of reducing all four species to subspecific or varietal status under P. glauca. The decision at this point appears to be more one of personal preference and usefulness rather than of biology. The author's preference is for the retention of the four species in the full recognition of areas of intergradation.

The spruce populations of 27 of the stands were rated Picea glauca (Table 6), three populations were rated Intermediate, and no populations were rated as P. engelmannii.

The populations with the highest index values occurred at the highest altitudes in Swan Hills. The correlation between spruce morphological index value and altitude is highly significant ($r = +0.68$, $P < 0.01$). Index values tended to decrease with decreasing altitude and greater distance from the Rocky Mountains. Populations with the lowest values were in the Christina highland (Figure 1).

This pattern of population composition is consistent with that found by earlier workers. Three previous studies in Alberta (Horton 1959, La Roi and Dugle 1968, Ogilvie and von Rudloff 1968) found that P. glauca populations occurred generally at altitudes below 1220 m, Intermediate populations between 1220 and 1830 m, and P. engelmannii

Table 6. Mean spruce morphological index values ($\bar{x}$) and standard deviations (s). *Picea glauca* = 1.00 - 1.66, Intermediate = 1.67 - 2.33, *P. engelmannii* = 2.34 - 3.00.

Stand	$\bar{x}$	s
6	2.05	0.75
7	1.85	0.76
29	1.68	0.75
9	1.64	0.69
8	1.62	0.69
10	1.61	0.64
14	1.53	0.62
15	1.52	0.60
12	1.49	0.63
27	1.45	0.61
28	1.45	0.60
22	1.45	0.59
11	1.44	0.59
19	1.39	0.60
13	1.38	0.54
24	1.37	0.57
21	1.37	0.56
30	1.36	0.54
23	1.35	0.58
5	1.35	0.57
17	1.35	0.51
20	1.33	0.60
18	1.31	0.50
26	1.29	0.53
16	1.29	0.51
25	1.28	0.45
3	1.24	0.50
2	1.18	0.41
4	1.15	0.37
1	1.09	0.30

populations above 1830 m. The highest populations sampled in this study were at 1295 m and were rated as Intermediate. All populations below 1220 m were rated as *P. glauca*.

Thus the spruce populations are basically *Picea glauca*, with varying amounts of introgression from *P. engelmannii*.

Fir

Much less work has been done on hybridization between *Abies balsamea* and *A. lasiocarpa*. Zavarin and co-workers (Zavarin and Snajberk 1965, 1972; Zavarin *et al.* 1970) have made chemosystematic studies of the two species, but a study of their intergradation has not been published.

Morphological evidence of natural hybridization in northern and central Alberta has been mentioned by Raup (1946) and Moss (1953, 1959), while Klaehn and Winieski (1962) have reported an artificial cross of *A. balsamea* with *A. lasiocarpa*. Boivin (1959) has recognized only one species, *Abies balsamea*, with two subspecies, *A. balsamea* ssp. *balsamea* and *A. balsamea* ssp. *lasiocarpa*. This situation is similar to that in spruce discussed above, and although Boivin's treatment of the two taxa indicates their close affinities, the author again thinks it preferable to maintain them as separate species.

Table 7 shows the fir morphological index values. Nineteen stand populations were rated as *Abies balsamea* and six populations were rated as Intermediate. Five stands contained no fir.

The populations with the highest values occurred at higher altitudes in Swan Hills. This pattern is similar to that of spruce,

Table 7. Mean fir morphological index values ($\bar{x}$) and standard deviations (s). Abies balsamea = 1.00 - 1.66, Intermediate = 1.67 - 2.33, A. lasiocarpa = 2.34 - 3.00.

Stand	$\bar{x}$	s
25	2.05	0.87
29	1.97	0.81
7	1.83	0.91
6	1.70	0.74
9	1.67	0.73
10	1.67	0.68
28	1.53	0.68
27	1.53	0.64
8	1.53	0.57
26	1.43	0.59
20	1.37	0.62
15	1.33	0.61
22	1.33	0.53
18	1.30	0.47
17	1.27	0.52
11	1.27	0.45
14	1.20	0.45
30	1.20	0.41
16	1.17	0.44
2	1.17	0.38
4	1.13	0.35
12	1.07	0.38
13	1.05	0.37
1	1.01	0.35
3	1.00	0.34

and corresponds to the report of Moss and Pegg (1963) of Abies lasiocarpa in Swan Hills. Index values tended to decrease with decreasing altitude and increasing distance from the Rocky Mountains. The correlation between fir morphological index and altitude, while significant ($r = +0.45$, $P < 0.05$), was not as high as that of spruce. Stands with Intermediate populations generally occurred at altitudes above 1200 m, while populations below 1200 m generally were rated as Abies balsamea. Populations with the lowest values were found in the Christina highland (Figure 1).

A notable deviation from this pattern was the population on Watt Mountain (Stand 25) which occurred at an altitude of 716 m and was rated as Intermediate. This stand was the most northerly studied (58° 40' N) and perhaps latitudinal compensation for altitude is important here.

The fir populations thus are basically Abies balsamea with varying amounts of introgression from A. lasiocarpa.

Pine

Natural hybrids between Pinus contorta and P. banksiana were first reported in 1929 (Austin 1929). Moss (1949) has presented morphological evidence of hybridization between the two species in central Alberta, while chemical evidence has been provided by Mirov (1956) and Zavarin et al. (1969). Artificial crosses between the two species have been made (Righter and Stockwell 1949), but neither species has been successfully crossed with any other species (Zavarin et al. 1969).

The populations of the stands on the Christina highland were rated as predominantly *Pinus contorta*. All stands west of the Christina highland were rated as wholly *P. contorta*.

Populations of mixed *Pinus contorta* and *P. banksiana* character were noted at lower elevations throughout northern and central Alberta, but in the highland areas the populations were either wholly or predominantly *P. contorta*. This pattern is consistent with the distribution reported by other workers (Moss 1949, 1959; Critchfield and Little 1966).

The cordilleran pine (*Pinus contorta*) appears to extend its influence farther east from the Rocky Mountains than either the cordilleran spruce (*Picea engelmannii*) or fir (*Abies lasiocarpa*).

A Geographic Index was computed by summing morphological index values for the three tree species complexes. Fir did not occur in five stands. Since the correlation between spruce morphological index value and fir morphological index value for the other 25 stands was highly significant ($r = +0.59$, $P < 0.01$), linear regression was used to estimate a fir morphological index value for stands 5, 19, 21, 23, and 24. For pine, the stands in the Christina highland were assigned a 2 (Intermediate), and all stands west of the Christina highland were assigned a 3 (*Pinus contorta*). The resulting Geographic Index is shown in Table 8.

Based on the three tree species only, the four stands in the Christina highland are Boreal, and the other 26 stands are Intermediate. A trend of increasing "boreality" is apparent from west to east and

Table 8. Geographic Index based on spruce, fir and pine. Boreal (3 - 5), Intermediate (5 - 7), Cordilleran (7 - 9).

Stand	Geographic Index
6	6.75
7	6.68
29	6.65
25	6.35
9	6.31
10	6.28
8	6.15
27	5.98
28	5.98
15	5.85
22	5.78
19	5.74
14	5.73
26	5.72
11	5.71
20	5.70
21	5.70
24	5.70
5	5.67
23	5.67
17	5.62
18	5.62
12	5.56
30	5.56
16	5.46
13	5.46
2	4.35
4	4.28
3	4.24
1	4.10

from high altitude to low altitude. The implications of the Geographic Index are discussed in the Geographic Relations section below.

VEGETATION CLASSIFICATION AND DESCRIPTION

Vegetational Units

The "community types" (Whittaker 1956, 1967; Langenheim 1962) recognized here are abstract vegetational units based on characteristics of concrete examples, _i.e._ the individual stands. The community types are viewed as "noda" (Poore 1962) along a vegetational gradient or "coenocline" (Whittaker 1967). A coenocline is paralleled by a gradient of environmental factors, the "complex-gradient" (Whittaker 1967). Another dimension is provided by a time or successional gradient.

The community types here delimited are based solely on vegetational (coenoclinal) characteristics. In contrast, some workers, _e.g._ Rowe (1956) and Sukachev (Sukachev and Dylis 1964) have recognized units, such as forest-types and biogeocoenoses, which combine the coenocline, the complex-gradient, and the successional gradient.

Classification

Initially, both cover and prominence values were used as a measure of species' performance. However, the use of frequency in the prominence value introduces a measure of dispersion. Thus the interpretation of the prominence value becomes unclear.

Both prominence value and cover were used in ordination and cluster analysis on a trial basis. The results from the use of prominence value were very similar to those produced by the use of cover, _i.e._ species with high cover values tend to have high promin-

ence values. Since no advantage could be seen in the use of prominence values, they have not been used, and all of the subsequent analyses and descriptions are based on cover alone.

The accuracy with which the two-dimensional cover ordination represented the similarity matrix was determined by computing a simple correlation coefficient between the interstand distance and the corresponding matrix dissimilarity value for all pairs of stands. A highly significant correlation ($r = +0.86$, $P < 0.01$) was found. The ordination was therefore considered to be an acceptable representation of the matrix.

Following ordination of the stands on the X and Y axes, cluster analysis was used to aid in the delimitation of community types. The cluster analysis produced five dendrograms, one for each technique of cluster formation. Three of the dendrograms were nearly identical (minimum variance, furthest neighbor, group average), and all five were similar. Figure 4 shows the minimum variance dendrogram. The cluster of Stands 6, 7, 8, 9, 10, and 29 was recognized by all five techniques, and agreed well with the position of these stands on the ordination field (Figure 5). A large cluster, consisting of stands 2, 3, 12, 13, 14, 16, 17, 19, 20, 21, 22, 23, 24, 27, and 30, was also recognized by all five techniques. These fifteen stands occupied an area together in the lower part of the ordination field (Figure 5).

The group (11, 25, 28) was clustered by all five techniques. Stands 4 and 26 were also clustered by all five techniques. Both of these groupings were consistent with the position of the stands on the ordination (Figure 5).

Figure 4. Cluster analysis dendrogram. Minimum variance technique of cluster formation (Pritchard and Anderson 1971).

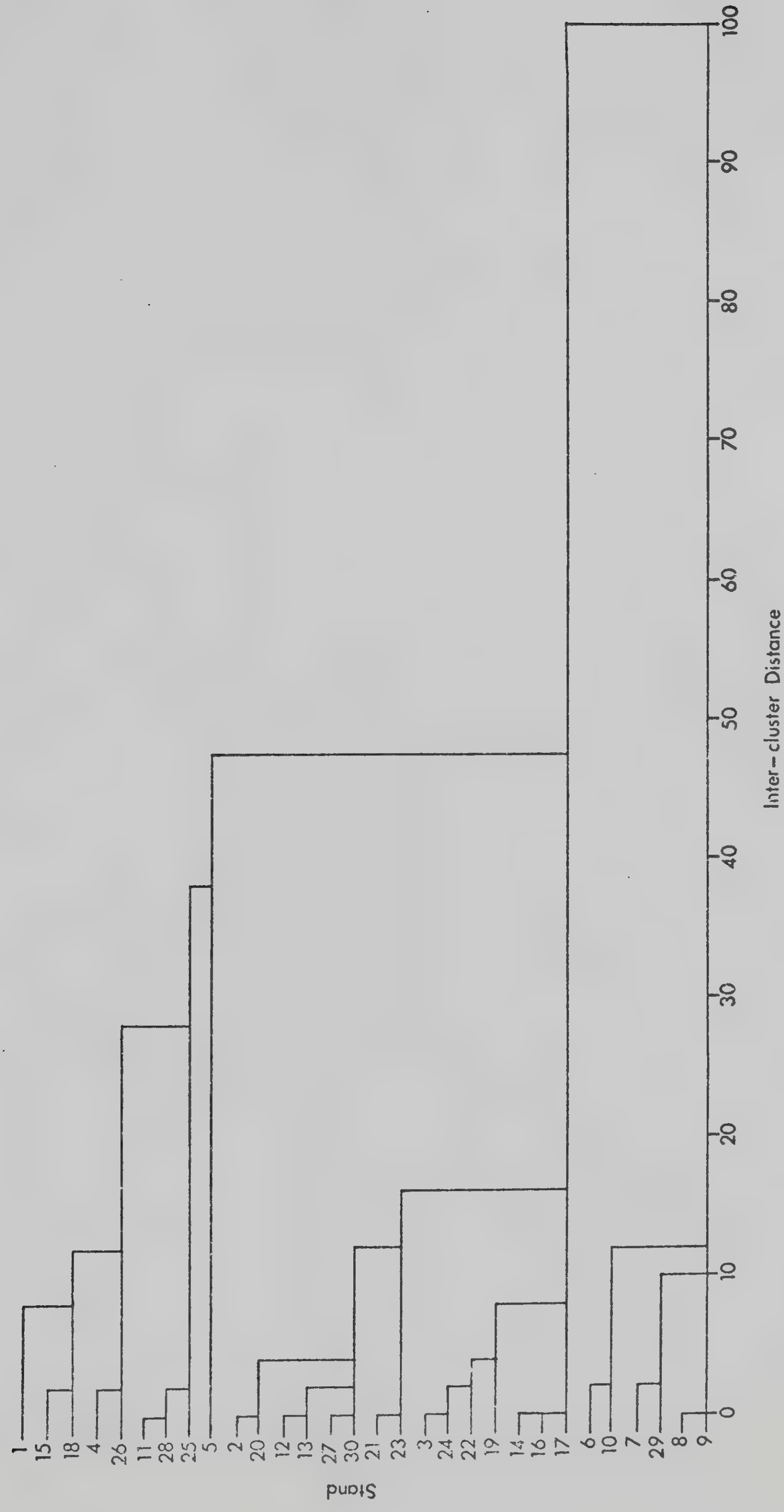
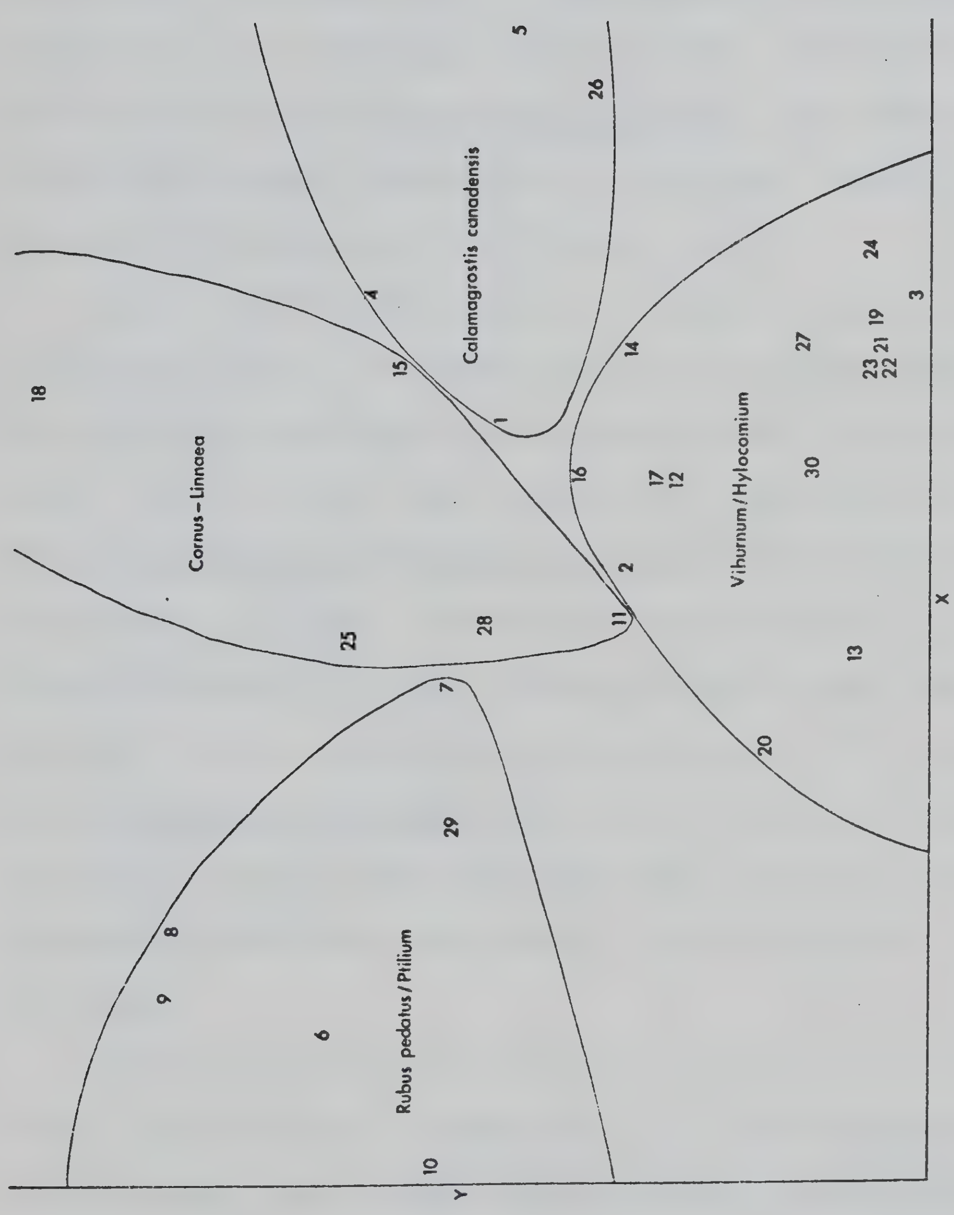

Stand
1
15
18
4
26
11
28
25
5
2
20
12
13
27
30
21
23
3
24
22
19
14
16
17
6
10
7
29
8
9
0
10
20
30
40
50
60
70
80
90
100
Inter-cluster Distance

Figure 5. The four community types on the ordination field.



Cornus – Linnaea
Calamagrostis canadensis
Viburnum / Hylocomium
Rubus pedatus / Ptilium
X
Y
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30

Stands 15 and 18 were joined to each other first in four of the dendrograms. They were then sometimes clustered with the 11, 25, 28 group and sometimes with the 4, 26 group. The position of stands 15 and 18 on the ordination (Figure 5) confirmed their relationship to each other, but helped little in resolving their relationship to either the 11, 25, 28 group or the 4, 26 group. However, stands 15 and 18 had relatively low Calamagrostis canadensis cover values (Table 9), thus differentiating them from the 4, 26 cluster. Stands 15 and 18 were therefore placed with stands 11, 25, and 28.

Stand 1 was sometimes joined with stands 15 and 18, and sometimes with stands 4 and 26. The mean cover value of Calamagrostis canadensis was relatively high (Table 9), thus placing stand 1 with the 4, 26 group. However, stand 1 also had relatively high mean cover values for Cornus canadensis and Linnaea borealis, and thus showed affinity with the 15, 18 cluster. Neither the position of stand 1 on the ordination (Figure 5) nor the similarity values between stand 1 and stands 4, 15, 18, and 26 helped resolve the matter. In the end, the high Calamagrostis canadensis mean cover was given greater weight. Consequently, stand 1 was placed with stands 4 and 26 in the full realization that stand 1 also showed a close affinity with stands 15 and 18.

Stand 5 was placed differently by all five techniques, but generally showed affinity to either the 11, 15, 18, 25, 28 group or the 1, 4, 26 group. Since it was closest to the 1, 4, 26 group on the ordination diagram (Figure 5) and also had the highest Calamagrostis

Table 9. Mean species cover by community type and stand. All species with >20% Presence (occurrence in at least six stands) are included, as well as a few species with < 20% Presence. See Appendix II for other species. t = < 1% cover, + = present.

	COMMUNITY TYPE AND STAND																													
	Rubus pedatus/ Ptilium						Cornus-Linnaea					Viburnum/Hylocomium															Calamagrostis canadensis			
SPECIES	8	9	6	10	7	29	11	28	25	15	18	2	20	12	13	27	30	3	24	22	19	14	16	17	21	23	1	4	26	5
Tree Layer																														
Abies balsamea	39	46	14	23	17	9	19	19	35	32	48	8	1	1	1	-	1	t	1	t	-	7	11	14	-	-	22	16	2	-
Picea glauca	6	5	4	t	26	15	23	16	18	28	14	29	36	44	37	31	40	38	43	50	50	41	53	39	58	68	23	28	43	35
Pinus contorta var. latifolia	3	2	17	20	2	t	2	-	-	-	t	-	17	6	16	5	-	-	-	-	-	t	-	-	t	-	2	t	-	1
Picea mariana	t	t	5	5	-	-	-	-	-	-	-	2	-	5	7	t	1	4	-	-	-	-	-	t	-	-	-	5	-	-
Populus tremuloides	-	-	-	-	-	-	t	-	-	8	8	2	5	6	11	-	3	9	1	5	20	5	9	t	24	3	9	-	1	5
Populus balsamifera	-	-	-	-	-	-	-	-	-	3	1	-	-	t	-	-	-	-	t	10	t	-	t	2	t	-	-	-	-	-
Betula papyrifera	-	t	-	-	-	-	-	t	3	-	1	t	t	t	t	-	-	t	t	-	-	2	t	4	-	t	2	t	11	10
Shrub Layer																														
Abies balsamea transgressives	13	11	8	43	6	13	11	7	3	7	2	5	1	2	5	3	2	-	-	1	-	9	4	7	-	-	10	8	1	-
Abies balsamea saplings	17	6	6	3	5	5	2	7	15	20	12	3	5	13	1	4	-	-	t	2	-	9	16	23	-	-	49	17	t	-
Picea glauca transgressives	t	t	-	-	t	2	-	7	-	1	-	-	3	t	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-
Picea glauca saplings	-	t	-	-	2	8	-	7	-	7	-	4	1	2	t	t	t	1	t	-	t	1	-	t	t	7	-	-	t	-
Rhododendron albiflorum	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Menziesia glabella	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ledum groenlandicum	4	10	8	9	-	-	-	t	-	-	-	-	t	t	-	t	t	-	-	-	-	-	-	-	-	-	-	-	-	-
Sorbus scopulina	t	t	t	t	t	t	-	t	t	t	1	-	t	-	-	-	t	-	-	-	t	t	t	-	-	-	-	2	-	t
Viburnum edule	-	-	-	-	-	-	5	t	2	28	10	13	7	18	9	4	t	20	23	34	19	29	22	22	23	12	15	9	9	3
Rosa acicularis	-	-	-	-	-	-	-	-	-	3	1	2	-	8	10	2	6	20	29	10	1	7	10	10	6	3	1	1	2	-
Rubus strigosus	-	-	-	-	t	-	1	t	3	t	2	t	-	t	-	6	-	2	2	-	1	t	1	1	-	-	1	12	13	12
Lonicera involucrata	-	-	-	-	t	-	-	-	-	3	3	-	-	2	1	-	2	5	4	-	-	12	11	11	-	-	4	4	-	2
Alnus crispa	-	-	-	-	-	-	-	-	-	-	-	-	3	t	-	1	t	-	2	-	9	1	t	t	-	t	4	-	-	-
Ribes lacustre	-	-	-	-	2	-	-	-	-	-	t	t	-	1	-	6	-	t	-	t	-	-	t	-	-	-	-	-	-	-
Ribes oxyacanthoides	-	-	-	-	-	4	-	-	-	1	-	-	-	-	-	-	1	-	2	-	-	t	-	-	-	-	-	-	-	-
Amelanchier alnifolia	-	-	-	-	-	-	-	-	-	t	-	-	-	t	-	-	-	1	t	-	t	t	t	t	-	-	-	-	-	-
Populus tremuloides transgressives	-	-	-	-	-	-	-	-	-	-	t	t	-	2	1	-	-	3	-	-	-	t	1	1	-	-	-	-	-	-
Oplopanax horridum	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1

Table 9 - Continued

COMMUNITY TYPE AND STAND

SPECIES	Rubus pedatus/ Ptilium						Cornus-Linnaea					Viburnum/Hylocomium															Calamagrostis canadensis			
	8	9	6	10	7	29	11	28	25	15	18	2	20	12	13	27	30	3	24	22	19	14	16	17	21	23	1	4	26	5
Herb-Dwarf Shrub Layer																														
Rubus pedatus	26	18	22	17	38	49	7	4	-	-	13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	23
Vaccinium membranaceum	10	22	-	t	23	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tiarella trifoliata	t	-	t	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Listera cordata	1	t	t	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Empetrum nigrum	t	t	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vaccinium caespitosum	-	-	13	16	-	18	-	-	-	-	-	-	8	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vaccinium myrtilloides	1	t	8	1	1	-	-	-	-	t	-	-	-	5	t	-	t	-	-	-	-	t	-	-	-	-	-	t	-	-
Ledum groenlandicum	1	4	3	-	-	-	-	-	-	-	-	1	-	9	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lycopodium obscurum var. dendroideum	-	-	-	-	12	-	-	-	-	1	-	-	t	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-
Moneses uniflora	-	t	-	-	-	-	-	t	-	-	t	-	-	-	-	t	t	t	-	-	-	t	-	t	-	-	-	-	-	-
Pyrola secunda	2	4	2	1	2	1	t	t	-	6	1	t	3	t	1	6	1	1	-	2	1	t	1	1	1	1	t	1	-	-
Vaccinium vitis-idaea var. minus	8	1	3	6	-	-	-	t	t	-	-	2	5	10	5	-	t	-	-	t	-	-	-	-	-	-	-	4	-	-
Lycopodium annotinum	4	5	4	3	-	9	t	2	8	3	8	6	4	13	2	-	t	4	-	-	-	2	t	1	-	-	2	11	2	-
Abies balsamea seedlings	4	8	-	1	1	4	7	3	2	10	3	1	1	t	1	1	-	-	-	t	-	2	t	1	-	-	5	2	-	-
Cornus canadensis	13	14	9	8	16	11	32	24	27	17	14	5	9	14	12	4	11	7	15	25	8	25	15	4	19	12	25	9	26	1
Linnaea borealis var. americana	4	11	3	2	8	6	41	32	12	6	11	7	7	10	17	4	6	28	9	17	9	9	8	12	14	20	13	2	-	t
Gymnocarpium dryopteris	2	-	-	-	-	-	-	3	-	t	20	-	-	5	-	t	3	-	-	-	-	2	2	t	-	-	-	1	-	2
Picea glauca seedlings	-	-	-	-	t	-	-	-	t	t	-	t	t	t	-	-	-	t	-	-	t	t	-	t	-	-	t	-	-	-
Rubus pubescens	-	-	-	-	-	-	8	6	2	14	7	2	t	7	2	2	12	11	6	26	3	12	10	6	11	4	9	10	3	3
Circaea alpina	-	-	-	-	-	-	t	t	-	-	-	t	-	-	-	-	-	-	t	-	-	-	-	-	-	-	1	2	-	-
Equisetum arvense	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	15	6	1	16	6	-	-	-	t	1	-	-	t	-	-
Mitella nuda	-	-	-	-	-	-	4	3	t	4	7	3	t	4	3	7	4	6	5	11	3	11	14	11	7	2	9	5	-	1
Mertensia paniculata	-	-	-	-	-	-	2	1	-	7	2	1	-	3	t	4	3	6	6	11	8	7	6	9	10	3	7	4	-	t
Maianthemum canadense var. interius-	-	-	-	-	-	-	t	5	1	5	3	2	1	3	7	-	-	-	2	-	5	1	1	t	3	t	4	t	2	t
Pyrola asarifolia	-	-	-	-	-	-	t	3	-	6	1	1	1	2	7	2	t	4	t	2	1	1	1	t	2	t	13	-	-	-
Viburnum edule	-	-	-	-	-	-	5	5	-	1	1	1	t	-	t	1	-	t	2	13	9	t	t	-	8	3	t	-	t	1
Rosa acicularis	-	-	-	-	-	-	1	1	-	2	t	3	-	1	1	2	1	1	8	10	6	1	1	-	6	5	t	1	2	-
Viola renifolia	-	-	-	-	-	-	t	2	-	1	t	-	1	1	1	-	2	t	3	6	t	1	1	2	5	-	-	-	-	1
Rubus strigosus	-	-	-	-	-	-	t	1	1	-	1	-	-	1	-	3	-	1	3	1	-	-	t	1	-	-	2	2	8	-
Actaea rubra	-	-	-	-	-	-	t	-	t	t	3	t	-	t	t	3	-	3	1	1	-	1	1	2	2	-	2	t	t	1
Fragaria virginiana var. glauca	-	-	-	-	-	-	-	-	-	t	-	-	-	t	-	-	1	2	1	2	1	2	t	t	-	1	-	t	-	t
Aster ciliolatus	-	-	-	-	-	-	-	-	-	t	t	-	-	-	-	-	6	2	-	-	2	1	t	t	-	-	t	-	-	-
Trientalis borealis	-	-	-	-	-	-	-	-	2	t	t	4	-	t	t	-	-	-	-	-	-	-	-	t	t	-	-	-	2	-

Table 9 - Continued

SPECIES	COMMUNITY TYPE AND STAND: Rubus pedatus/Ptilium						Cornus-Linnaea					Viburnum/Hylocomium															Calamagrostis canadensis			
	8	9	6	10	7	29	11	28	25	15	18	2	20	12	13	27	30	3	24	22	19	14	16	17	21	23	1	4	26	5
H - D S Layer (cont.)																														
Dryopteris spinulosa	-	-	-	-	-	-	2	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	1	1	-
Galium boreale	-	-	-	-	-	-	-	-	-	2	-	t	-	1	t	-	t	1	1	-	-	-	1	1	1	t	-	t	-	-
Galium triflorum	-	-	-	-	-	-	t	1	-	t	1	-	-	t	-	1	1	-	2	-	-	t	t	t	t	-	t	t	t	t
Viola rugulosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	1	-	-	-	-	-	-
Goodyera repens	-	-	-	-	-	-	-	-	-	-	-	t	-	t	t	-	1	-	-	-	-	t	1	t	1	t	-	-	-	-
Arnica cordifolia	t	-	-	-	-	-	t	2	-	-	t	-	1	-	t	1	-	-	-	-	1	-	-	-	-	-	-	-	-	t
Ribes triste	-	-	-	-	-	t	-	1	-	-	-	1	-	t	-	-	-	t	3	2	t	-	1	-	t	t	-	-	-	-
Pyrola virens	t	-	-	t	t	-	t	-	-	-	t	t	1	-	t	-	-	t	-	-	-	t	-	1	-	1	1	-	-	-
Ribes glandulosum	-	-	-	-	1	-	t	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	2	t
Ribes lacustre	-	-	-	-	1	-	1	-	-	-	t	t	-	t	-	1	-	-	-	3	-	-	t	-	-	t	-	-	t	2
Lathyrus ochroleucus	-	-	-	-	-	-	-	-	-	t	-	t	-	2	t	-	-	2	2	t	2	1	-	t	1	t	-	-	-	5
Equisetum sylvaticum	1	-	6	-	3	3	1	2	-	2	2	2	-	2	8	-	-	2	-	-	-	-	1	1	-	4	4	8	-	2
Petasites palmatus	1	-	t	-	1	t	4	t	t	4	1	2	t	2	4	-	1	3	t	2	2	3	4	1	4	5	5	1	-	3
Epilobium angustifolium	t	-	-	t	t	1	-	3	t	2	-	-	t	1	-	4	t	5	t	3	3	2	t	-	2	t	1	1	t	8
Dryopteris assimilis	1	-	-	-	t	t	-	t	-	-	1	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	6
Calamagrostis canadensis	1	-	t	t	7	2	2	5	1	2	3	-	-	6	2	9	1	13	2	-	t	10	-	1	6	t	21	30	27	86
Aralia nudicaulis	-	-	-	-	-	-	-	11	t	9	17	8	-	12	3	-	8	1	6	t	1	14	23	5	-	t	15	8	14	16
Streptopus amplexifolius	1	-	2	-	3	3	1	2	-	t	1	-	-	-	-	t	t	t	-	-	-	t	-	-	-	-	1	2	-	12
Bryoid Layer																														
Ptilium crista-castrensis	33	42	36	42	39	36	13	31	26	3	5	5	9	16	27	12	16	10	3	5	1	8	17	19	7	4	16	5	1	t
Pleurozium schreberi	43	39	46	36	24	14	19	11	3	2	4	30	40	13	13	1	15	5	t	9	12	10	25	15	10	12	14	2	2	1
Hylocomium splendens	27	23	13	11	17	32	50	36	53	11	4	52	43	38	50	38	35	32	38	38	27	17	18	29	71	58	24	9	3	13
Polytrichum commune	2	t	1	-	t	3	t	1	-	-	t	-	-	t	2	-	-	-	-	-	-	-	-	-	-	-	1	2	-	-
Dicranum acutifolium	-	t	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dicranum scoparium	-	-	t	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dicranum polysetum	1	-	1	4	-	t	t	-	-	-	-	-	-	1	2	-	1	t	-	-	-	t	-	-	-	-	-	-	-	t
Dicranum fuscescens	t	2	t	t	t	t	t	t	t	2	t	t	-	t	-	-	t	-	-	-	-	-	-	-	-	t	t	-	-	-
Plagiomnium medium	-	-	-	-	-	-	-	8	-	12	7	1	-	2	-	2	-	1	-	-	-	6	4	3	-	-	2	t	-	-
Brachythecium salebrosum	-	-	-	-	-	-	-	-	-	t	t	t	-	t	t	3	-	3	-	t	-	4	2	t	t	-	5	t	t	t

Table 9 - Continued

	COMMUNITY TYPE AND STAND																													
	Rubus pedatus/ Ptilium						Cornus-Linnaea					Viburnum/Hylocomium															Calamagrostis canadensis			
SPECIES	8	9	6	10	7	29	11	28	25	15	18	2	20	12	13	27	30	3	24	22	19	14	16	17	21	23	1	4	26	5
Bryoid Layer (cont.)																														
Mnium spinulosum	-	-	-	-	-	-	t	-	t	t	t	t	-	-	t	-	t	t	-	-	-	-	t	-	-	-	-	-	t	-
Plagiomnium drummondii	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	t	-	-	t	-	t	t	t	-	-	t	-	-	-
Plagiomnium cuspidatum	-	-	-	-	-	-	-	-	-	t	-	t	-	-	-	-	-	t	t	-	t	t	-	t	-	-	-	-	1	-
Ceratodon purpureus	-	-	-	-	-	-	-	-	-	-	-	t	-	t	-	-	-	1	-	-	-	t	-	t	-	t	-	-	-	-
Pylaisiella polyantha	-	-	-	-	-	-	-	-	-	t	-	-	-	-	t	-	-	-	-	-	-	t	t	t	t	-	t	-	-	t
Eurhynchium pulchellum	-	-	-	-	-	-	-	-	-	t	-	t	-	t	t	-	t	t	1	-	1	t	t	t	t	1	-	-	-	-
Peltigera aphthosa	t	t	t	1	-	t	t	t	-	-	-	-	-	-	-	-	-	t	t	-	1	-	t	t	t	t	-	-	-	-
Pohlia nutans	t	t	t	-	t	t	-	-	t	-	-	t	-	t	-	-	t	t	-	t	t	-	-	-	-	-	t	-	-	-
Dicranum fragilifolium	-	t	-	-	-	t	t	t	-	-	-	t	-	t	t	-	t	-	t	t	-	-	t	t	t	-	-	-	-	-
Polytrichum juniperinum	t	t	t	-	t	-	-	-	-	1	-	-	-	-	-	-	t	-	-	-	t	-	t	t	-	t	-	-	-	-
Cladonia coniocraea	-	-	t	-	t	-	t	t	t	-	t	-	-	-	-	-	-	t	-	-	t	t	-	-	-	-	-	-	-	-
Ptilidium pulcherrimum	-	t	-	t	t	t	t	t	-	t	t	-	-	-	-	-	t	-	t	t	-	-	t	t	-	t	-	-	-	-
Drepanocladus uncinatus	-	t	-	-	-	-	-	-	-	t	t	t	-	t	-	-	t	t	t	t	t	t	t	t	-	-	t	-	-	t
Epiphytes																														
Platismatia glauca	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hypogymnia bitteri	+	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Alectoria fremontii	+	+	-	+	+	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Parmeliopsis ambigua	+	+	+	+	-	+	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Cetraria pinastri	-	-	+	+	-	-	-	-	-	-	-	+	-	-	-	-	+	-	+	-	-	-	-	-	+	-	-	-	-	-
Alectoria implexa	+	+	-	+	-	-	-	+	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-	-	+	-	-
Parmelia sulcata	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Usnea subfloridana	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+	+	+	+	+	+	-
Evernia mesomorpha	+	+	-	+	-	+	+	+	+	+	+	+	+	+	-	+	+	+	+	+	+	+	+	+	+	+	+	-	+	-
Usnea scabrata	+	+	+	+	+	+	+	+	+	-	+	+	-	+	+	+	+	-	+	+	+	-	-	-	+	+	+	-	-	-
Usnea alpina	-	-	+	-	-	-	-	-	+	+	-	+	+	+	-	-	+	+	-	-	+	+	+	-	+	+	+	+	+	-
Ramalina pollinaria	+	-	-	-	-	+	-	-	-	+	-	+	-	+	-	-	+	+	+	+	+	+	+	+	-	+	-	-	+	-
Alectoria americana	+	-	+	-	+	-	-	-	-	-	-	+	-	+	-	+	+	-	-	-	-	+	-	-	-	-	-	+	-	-
Hypogymnia physodes	+	+	+	+	-	+	+	+	-	+	+	+	-	+	-	+	+	+	+	+	+	+	+	+	+	-	-	+	-	+
Alectoria glabra	+	+	+	+	+	-	+	+	-	-	+	-	+	+	-	-	+	+	-	-	-	+	-	-	-	-	-	+	-	-
Ramalina crinalis	+	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-	-	-	+	+	+	-	-	-	-	-	-
Parmelia elegantula	-	-	-	-	+	-	-	-	-	-	-	+	-	-	+	-	-	+	+	-	-	+	+	-	-	-	-	-	-	-
Cetraria halei	+	+	+	+	-	+	+	+	-	-	-	-	+	+	-	+	+	-	-	+	-	-	-	-	+	-	-	-	-	-
Usnea hirta	+	-	-	+	-	-	-	-	+	+	+	-	-	-	-	+	-	+	-	-	-	-	+	-	+	+	-	-	-	-
Usnea sorediifera	-	-	+	-	-	-	+	+	-	+	+	-	+	-	-	-	-	+	-	-	+	-	-	-	-	-	-	-	-	-
Orthotrichum speciosum var. elegans	-	-	-	-	-	-	-	-	-	+	+	-	-	-	+	-	-	-	-	-	-	+	+	+	-	+	-	-	-	-
Ramalina fastigiata	-	-	-	-	-	-	+	-	-	-	-	-	+	+	+	-	+	-	+	+	+	-	-	-	-	-	-	+	-	-

canadensis mean cover value of any stand, it was grouped with stands 1, 4, and 26.

Thus the final delimitation was into four community types which are shown on the ordination field in Figure 5. The groupings provided by the minimum variance, furthest neighbor, and group average clustering techniques were closest to the final delimitation. Pritchard and Anderson (1971) also found these three techniques to be most useful.

Rubus pedatus/Ptilium community type

Stands with the understory dominated by Rubus pedatus and Ptilium crista-castrensis occurred in Swan Hills at the highest altitudes studied (1220-1295 m).

The stands were generally open (Figure 6) with a mean tree cover of 43%, the lowest of the four community types. Abies balsamea and Picea glauca accounted for 21% and 13% respectively. The tree layer of this community type was almost entirely coniferous, and four of the six stands were dominated by Abies balsamea. Other mean cover amounts were: Pinus contorta (7%), Picea mariana (2%), and Betula papyrifera s.l. (<1%). Mean tree density was 1005 stems/ha, and total basal area (Table 10) averaged 39.1 m^2/ha. Neither Populus tremuloides nor P. balsamifera were present in this type, since they become a very minor element above about 915 m in Swan Hills. Both Abies balsamea and Pinus contorta reach their highest cover here.

Figure 6. *Rubus pedatus/Ptilium* community type (Stand 29).

Table 10. Mean basal area (m^2/ha) of the tree species by community type.

Species	Community type: *Rubus pedatus*/*Ptilium*	*Cornus*-*Linnaea*	*Viburnum*/*Hylocomium*	*Calamagrostis canadensis*
Picea glauca	15.0	20.2	40.0	24.6
Abies balsamea	17.8	20.8	2.2	5.9
Pinus contorta	4.3	0.9	2.9	0.7
Populus tremuloides	----	5.7	24.5	3.6
P. balsamifera	----	1.4	1.1	----
Betula papyrifera s.l.	----	0.7	0.5	2.3
Picea mariana	2.0	----	1.0	0.8
Total	39.1	49.7	72.2	37.9

Figure 7. Regression lines of *Picea glauca* diameter growth rate in the four community types. ($y = a + bx$, where y = age (years at breast height) and x = dbh).

a. *Rubus pedatus/Ptilium* community type ($r = +0.64$, $P<0.01$, $n = 36$).

b. *Cornus-Linnaea* community type ($r = +0.38$, $P<0.05$, $n = 31$).

c. *Calamagrostis canadensis* community type ($r = +0.36$, $P = 0.05$, $n = 29$).

d. *Viburnum/Hylocomium* community type ($r = +0.45$, $P<0.01$, $n = 156$).

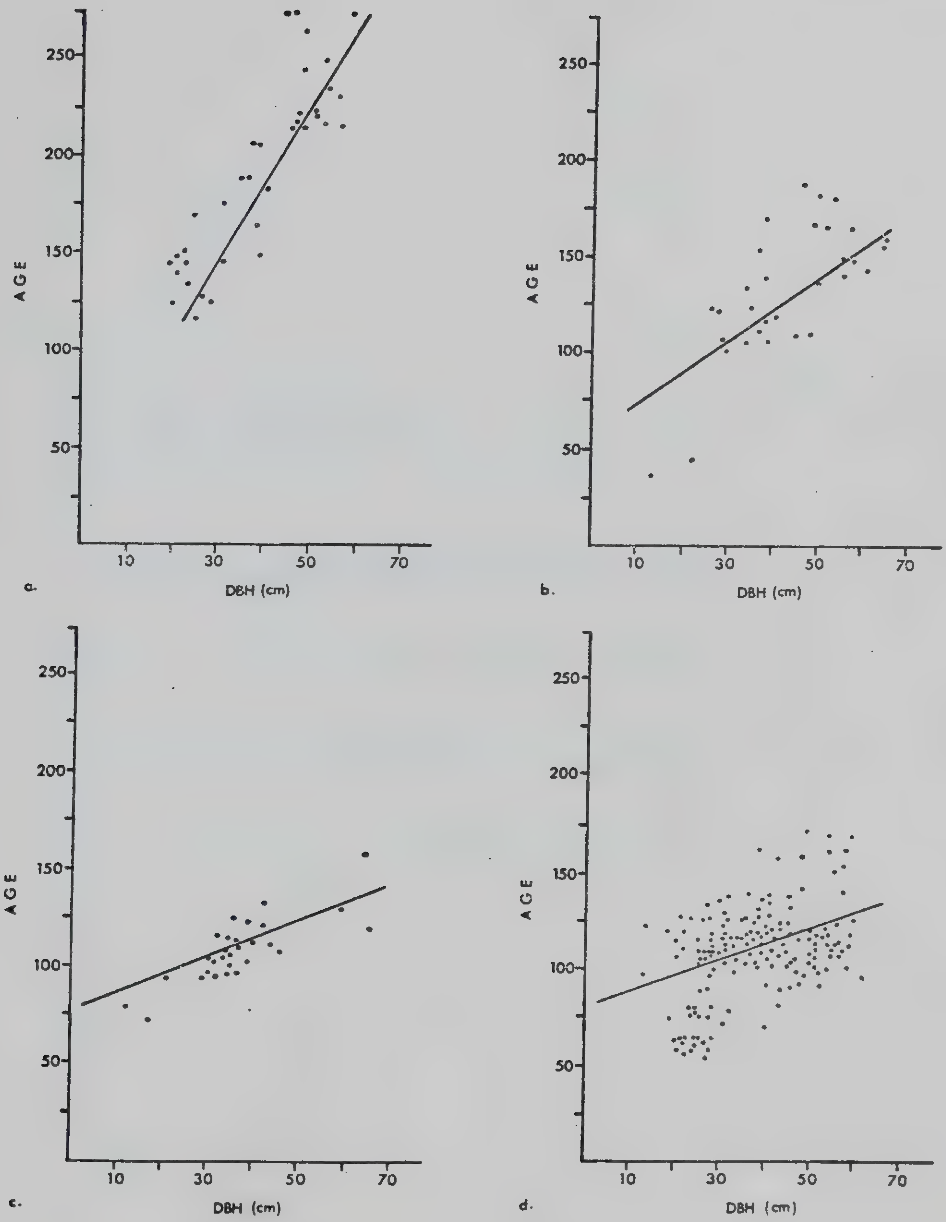

AGE
250
200
150
100
50
10
30
50
70
DBH (cm)
a.
b.
c.
d.

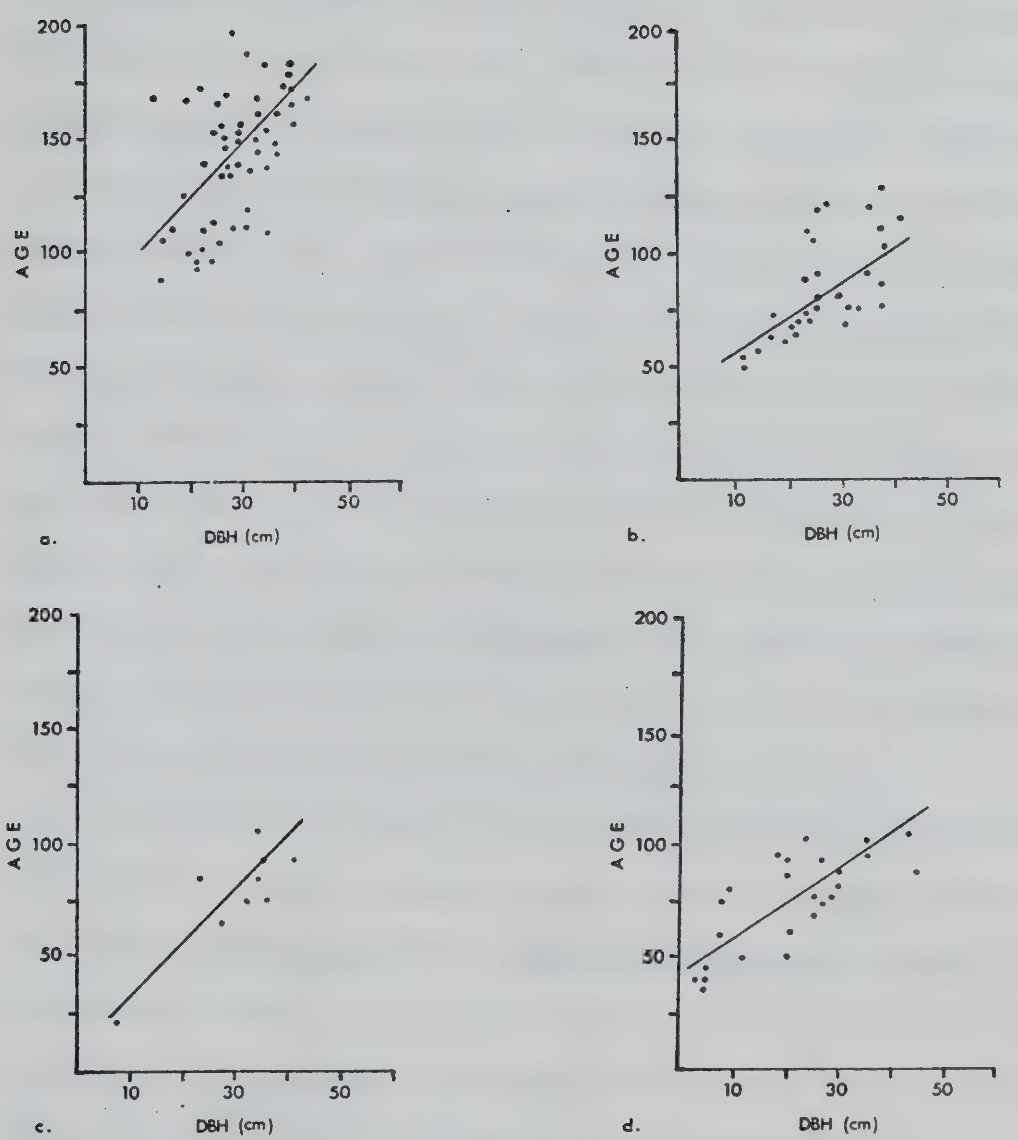
Figure 8. Regression lines of *Abies balsamea* diameter growth rate in the four community types. ($y = a + bx$, where y = age (years at breast height) and x = dbh).

a. *Rubus pedatus/Ptilium* community type ($r = +0.64$, $P<0.01$, $n = 53$).

b. *Cornus-Linnaea* community type ($r = +0.55$, $P<0.01$, $n = 31$.

c. *Calamagrostis canadensis* community type ($r = +0.71$, $P<0.05$, $n = 9$.

d. *Viburnum/Hylocomium* community type ($r = +0.71$, $P<0.01$, $n = 26$).



200
150
100
50
AGE
10
30
50
a.
DBH (cm)
b.
c.
d.

The mean morphological index values of both spruce and fir (1.74 and 1.73) were highest in this type, indicating maximum influence of the cordilleran *Picea engelmannii* and *Abies lasiocarpa*. Three of the spruce populations of this community type were rated Intermediate. The other three populations were rated as *P. glauca*, but had index values above 1.61. Five of the fir populations were rated Intermediate while Stand 8 (1.53) was rated *Abies balsamea*.

The stands of the *Rubus pedatus*/*Ptilium* community type were the oldest studied, with a mean stand age of 216 years. The diameter growth rates for *Picea glauca* (Figure 7) and *Abies balsamea* (Figure 8) were significantly lower (t test) than those of the other community types. Whether tree density or physical environmental factors are responsible for this is not clear. However, since the mean tree density (1005 stems/ha) is comparable to that of the *Cornus*-*Linnaea* (905 stems/ha) and *Viburnum*/*Hylocomium* (1015 stems/ha) community types, it appears that physical environmental factors of climate (Table 4) and soil nutrients are influential.

Mean total shrub cover was 36% with *Abies balsamea* transgressives providing 15%. Other prominent species were *A. balsamea* saplings (7%) and *Ledum groenlandicum* (5%). *Ledum groenlandicum* had highest cover here, being present in only trace amounts in the other types. *Menziesia glabella* and *Rhododendron albiflorum* occurred only in this type, and *Viburnum edule* and *Rosa acicularis* were completely absent.

Mean total cover of the herb-dwarf shrub layer was 88%. *Rubus pedatus* was dominant with 28% cover, followed by *Cornus canadensis* (12%), *Vaccinium membranaceum* (9%), and *V. caespitosum* (8%). *Vaccinium*

membranaceum and Tiarella trifoliata were found only in this type, while a number of species were notable by their complete absence, e.g. Aralia nudicaulis, Rubus pubescens, Mitella nuda, Mertensia paniculata, Maianthemum canadense var. interius, and Pyrola asarifolia.

Bryoid cover averaged 95%, highest of the four community types. Nearly all the bryoid cover was contributed by the three feather mosses, Ptilium crista-castrensis (38%), Pleurozium schreberi (34%), and Hylocomium splendens (21%). Eight species of terrestrial mosses and lichens were found only in this community type: Dicranum acutifolium, D. scoparium, Polytrichum piliferum, Cetraria nivalis, C. ericetorum, Cladonia cornuta, C. phyllophora, Cladina alpestris. The community type was further distinguished by the absence of several species which were common to the other three community types, e.g., Plagiomnium medium, Mnium spinulosum, Brachythecium salebrosum. Ptilium crista-castrensis and Dicranum polysetum reached peak cover here.

Six species of epiphytic lichens were found only in this community type: Platismatia glauca, Hypogymnia bitteri, H. tubulosa, Usnea dasypoga, Physcia adscendens, Alectoria pseudofuscescens.

The soils were Dystric Brunisols, Orthic Grey Luvisols and Bisequa Humo-Ferric Podzols developed mostly on residual Tertiary parent materials.

Cornus-Linnaea community type

This type (Figure 9) occurred at intermediate altitudes of 716 - 1112 m (mean 957 m).

Total tree cover averaged 57%. Abies balsamea (31% cover) was

Figure 9. Cornus-Linnaea community type (Stand 25).

dominant. Other trees present were: Picea glauca (20%), Populus tremuloides (3%), Betula papyrifera s.l. (1%), Populus balsamifera (1%), and Pinus contorta (<1%). Mean tree density was 905 stems/ha, and mean total basal area was 49.7 m^2/ha.

Mean spruce and fir morphological index values were 1.41 and 1.50, respectively. Mean stand age was 133 years.

Mean total shrub cover was 31%, lowest of the four types. Abies balsamea saplings were dominant (11%), followed by Viburnum edule (9%), A. balsamea transgressives (6%), Lonicera involucrata (2%) and Picea glauca saplings (2%).

The herb-dwarf shrub layer had a mean total cover of 103%. Major species were: Cornus canadensis (23%), Linnaea borealis var. americana (20%), Rubus pubescens (7%), Aralia nudicaulis (6%), R. pedatus (5%), and Gymnocarpium dryopteris (5%). Cornus canadensis, Linnaea borealis and Gymnocarpium dryopteris attained maximum cover in this type.

Mean total bryoid cover was 63%. Major species were Hylocomium splendens (31%), Ptilium crista-castrensis (16%), Pleurozium schreberi (8%), and Plagiomnium medium (5%). Plagiomnium medium reached peak cover here. Four terrestrial bryoids occurred only in this type: Plagiomnium rugicum, Isopterygium elegans, Nephroma resupinatum, Cladonia chlorophaea.

The soils were all Orthic Grey Luvisols developed either on till or till mixed with residual deposits.

The Cornus-Linnaea community type appears to be intermediate between the nearly pure conifer forests of the Rubus pedatus/Ptilium community type and the mixedwood forests of the Viburnum/Hylocomium community type. The intermediate nature of this community type is supported by floristic composition (including tree morphological index values), position on the ordination field (Figure 5), and the geographic and altitudinal locations of the stands.

Viburnum/Hylocomium community type

This was the most frequently sampled community type, being represented by fifteen stands (Figure 10). The type occurred over a broad geographic range at altitudes of 579 to 1113 m. The mean altitude was 816 m, making it the lowest type.

Mean total tree cover was 60%, the maximum obtained. Picea glauca reached maximum cover (49%), and was dominant, followed by Populus tremuloides (7%), Abies balsamea and Pinus contorta (each 3%), and Betula papyrifera s.l., Picea mariana, and Populus balsamifera (1% each). This community type had the highest mean tree density (1015 stems/ha) and mean total basal area (72.2 m^2/ha).

The mean spruce and fir morphological index values (1.37 and 1.21) indicate a comparatively small amount of introgression from the cordilleran species.

Mean stand age was lowest at 115 years. The rates of Picea glauca and Abies balsamea diameter growth were not significantly different (t test) from those of the Cornus-Linnaea and Calamagrostis canadensis community types.

Figure 10. Viburnum/Hylocomium community type (Stand 30).

Mean total shrub cover was 42%, with Viburnum edule contributing 17%, Rosa acicularis 8%, Abies balsamea saplings 5%, Lonicera involucrata 3%, and A. balsamea transgressives 3%. Viburnum edule, Rosa acicularis, and Ribes lacustre all reached peak mean cover values.

Mean total herb-dwarf shrub cover was lowest (87%) although quite comparable to the Rubus pedatus/Ptilium community type (88%). Cornus canadensis was dominant with a mean cover of 13%, followed by Linnaea borealis (12%), Rubus pubescens (7%), Mitella nuda (6%), Aralia nudicaulis (5%), and Mertensia paniculata (5%).

Bryoid cover averaged 67%. The main species were Hylocomium splendens (39%), Pleurozium schreberi (14%), and Ptilium crista-castrensis (10%). Hylocomium splendens had highest cover here. Eight species of terrestrial bryoids, e.g. Peltigera polydactyla, Dicranum pallidisetum, Plagiomnium rostratum, and five species of epiphytes, e.g. Ramalina minuscula, Anaptychia speciosa, Parmelia septentrionalis, occurred only in this type.

The soils were predominantly Orthic Grey Luvisols developed on till.

Calamagrostis canadensis community type

Stands of this community type occurred over a broad geographic range at altitudes of 488 - 1113 m (mean altitude 831 m). The altitudinal range is comparable to that of the Viburnum/Hylocomium and Cornus-Linnaea community types.

The stands were generally open (Figure 11) and had the lowest mean tree density (530 stems/ha). The tree layer had a mean cover of 54%, the bulk of which was provided by Picea glauca (32%) and Abies balsamea

Figure 11. Calamagrostis canadensis community type (Stand 4).

(10%). Betula papyrifera s.l. had a mean cover of 6%, Populus tremuloides 4%, and Pinus contorta and Picea mariana contributed 1% each. Betula papyrifera s.l. had maximum cover in this type. The mean spruce and fir morphological index values (1.22 and 1.19) were lowest here. Total basal area averaged 37.9 m^2/ha, with Picea glauca and Abies balsamea contributing the most. Mean stand age was 119 years, slightly older than that of the Viburnum/Hylocomium community type (115 years).

Mean total shrub cover was 43%, about the same as the Viburnum/Hylocomium community type (42%). Abies balsamea saplings were dominant with a mean cover of 17%, followed by Viburnum edule (9%), and Rubus strigosus (6%). Rubus strigosus and Sorbus scopulina reached their highest cover here.

The herb-dwarf shrub layer had a mean total cover of 126%, highest of the four community types. Calamagrostis canadensis (41% cover) was dominant, followed by Cornus canadensis (15%), Aralia nudicaulis (13%), and Rubus pubescens (6%). The following species reached peak cover: Calamagrostis canadensis, Aralia nudicaulis, Epilobium angustifolium, Dryopteris assimilis, D. spinulosa, Equisetum sylvaticum and Streptopus amplexifolius. Although the high total cover values of both the herb-dwarf shrub and the shrub layer would seem to be related to the low tree density, no significant correlation was obtained. Total tree cover, however, is not much different from the other community types.

Mean total bryoid cover was lowest (29%) in this type. The relatively high total cover of the shrub and herb-dwarf shrub layers apparently makes conditions less favorable for the terrestrial bryoids.

Hylocomium splendens was dominant (12%) followed by *Ptilium crista-castrensis* (5%) and *Pleurozium schreberi* (5%). *Parmelia exasperatula*, an epiphytic lichen, and *Cladonia cenotea*, a terrestrial lichen, occurred only in this community type. The following six species of cryptogams were absent, although they occurred in the other three community types: *Dicranum fragilifolium*, *Rhytidiadelphus triquetris*, *Ptilidium pulcherrimum*, *Cladonia coniocraea*, *Cetraria halei*, *Usnea hirta*.

The soils were all Orthic Grey Luvisols developed on till and residual Tertiary deposits.

The *Calamagrostis canadensis* community type shows a close relationship most particularly to the *Cornus-Linnaea* community type, but also to the *Viburnum/Hylocomium* community type.

Conclusions

The nearly pure conifer, higher altitude *Rubus pedatus/Ptilium* community type and the mixedwood, lower altitude *Viburnum/Hylocomium* community type form the two best defined types.

The *Cornus-Linnaea* community type appears transitional between the two main types, and is not as clear-cut a grouping.

The *Calamagrostis canadensis* community type is perhaps a category of smaller magnitude than the other three community types. A case could be made for combining the *Calamagrostis canadensis* and *Cornus-Linnaea* community types into one group, or for making a *Calamagrostis canadensis* sub-type under the *Cornus-Linnaea* community type. Further studies may show this to be a better solution, but for the present the

four community types will be retained bearing in mind their relative strengths and weaknesses.

ENVIRONMENTAL RELATIONS

The relationships between vegetational and environmental variables were examined by plotting environmental variables on the ordination field, and by simple correlation analysis. Although only a few environmental factors were measured, several appear to be important in determining vegetation pattern. Significant correlation between vegetational and environmental factors is only suggestive of causality, not proof. Two variables are often correlated by virtue of their common correlation with a third, frequently unknown, variable.

The criteria used for stand selection restricted the amount of physiographic variation among stands and no relation was found between most of the physiographic variables (*e.g.* slope gradient, aspect) and vegetational variables. However, altitude showed both a distinct pattern on the ordination field (Figure 12) and significant correlation with several vegetational variables (Table 11). Altitude *per se* is probably not important causally, but rather it appears that other factors, which are correlated with both elevation and the vegetational variables, should be considered as possible causal factors.

Precipitation increases and temperature decreases with increasing altitude in the study area (Table 4, Muttit 1961, MacIver 1970). There appears to be a trend of decreasingly favorable moisture conditions from the upper left of the field in the *Rubus pedatus*/*Ptilium* community type, to the lower right, in the *Viburnum*/*Hylocomium* community type.

Figure 12. Stand altitude on the ordination field. 1 = <700 m, 2 = 700 - 1200 m, 3 = >1200m. Actual values in Table 5.

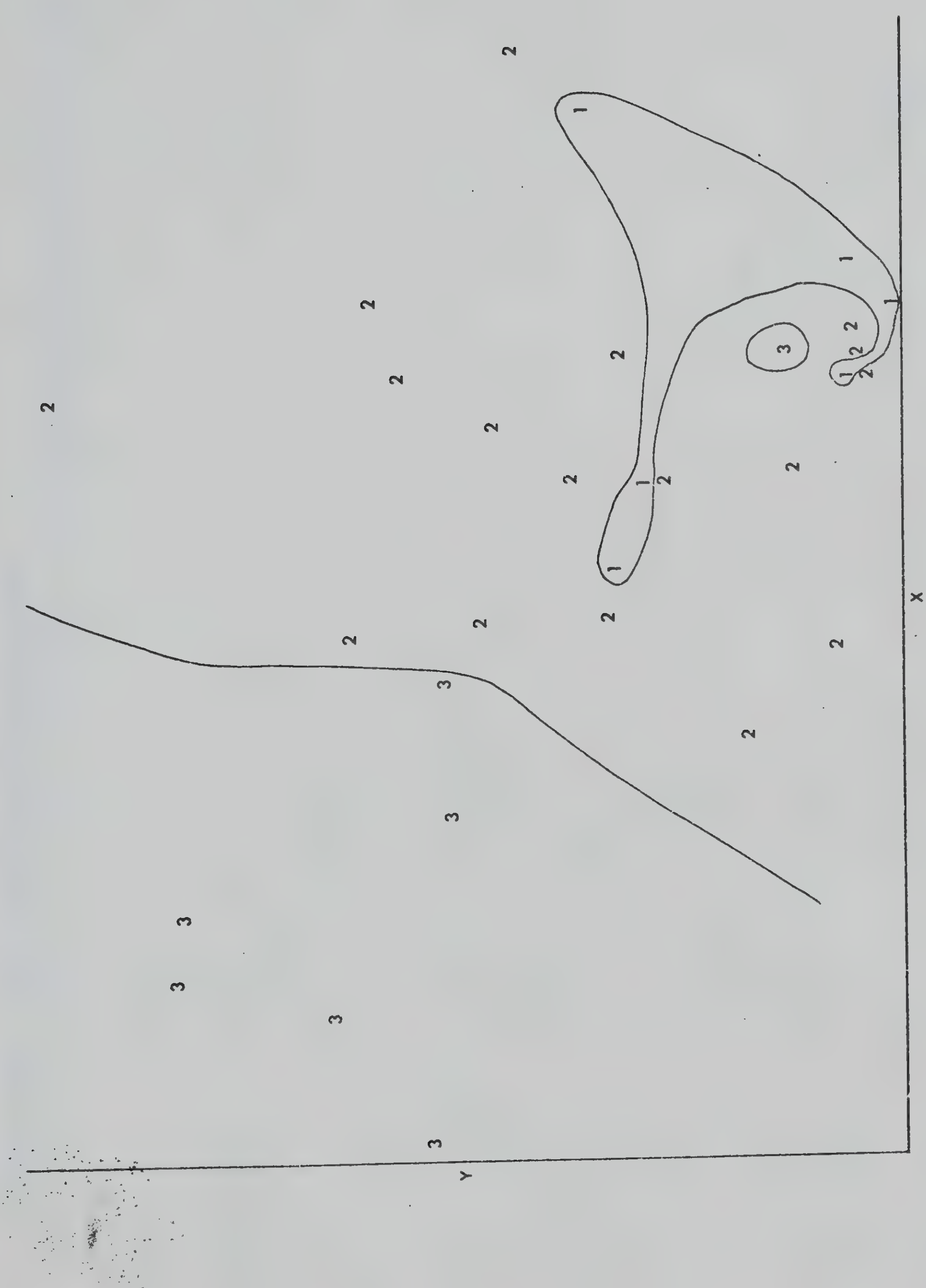

X
Y

Table 11. Simple correlation coefficients (r) of selected vegetational and environmental variables. r = ±0.36 for P = 0.05, r = ±0.46 for P = 0.01. TEC = total exchange capacity.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Picea glauca cover	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Abies balsamea cover	2	-.70	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pinus contorta cover	3	-.36	—	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Populus tremuloides cover	4	—	—	—	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Viburnum edule cover	5	+.63	—	—	+.51	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ledum groenlandicum cover	6	-.61	+.42	+.51	—	—	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rubus pedatus cover	7	-.52	—	—	—	-.57	+.37	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
R. pubescens cover	8	+.37	—	-.40	+.36	+.72	-.37	-.46	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Linnaea borealis cover	9	—	—	—	—	—	—	—	—	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cornus canadensis cover	10	—	—	—	—	—	—	—	+.42	+.55	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Calamagrostis canadensis cover	11	—	—	—	—	—	—	—	—	—	—	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ptilium crista-castrensis cover	12	-.66	+.40	+.42	—	-.61	+.64	+.62	-.46	—	+.42	—	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pleurozium schreberi cover	13	-.39	—	+.55	—	-.39	+.69	+.37	-.43	—	—	-.38	+.61	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hylocomium splendens cover	14	+.39	-.36	—	—	—	—	—	—	+.49	—	—	—	—	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Total tree cover	15	+.51	—	—	+.73	+.54	—	-.52	—	—	—	—	—	—	—	.	.	.	.	.	.	.	.	.	.	.	.	.
Total shrub cover	16	—	—	—	—	+.63	—	—	+.39	—	—	—	—	—	—	—	.	.	.	.	.	.	.	.	.	.	.	.
Total herb-dwarf shrub cover	17	—	—	-.37	—	—	—	—	+.45	—	—	+.57	—	-.41	—	—	—	.	.	.	.	.	.	.	.	.	.	.
Total bryoid cover	18	—	—	+.46	—	-.41	+.47	—	-.40	—	—	-.56	+.73	+.76	+.49	—	—	-.44	.	.	.	.	.	.	.	.	.	.
Effective stand age	19	-.57	+.38	—	-.45	-.48	+.52	+.73	—	—	—	—	+.66	—	—	-.39	—	—	—	.	.	.	.	.	.	.	.	.
Altitude	20	-.65	+.44	+.40	—	-.64	+.54	+.71	-.38	—	—	—	+.78	+.48	—	-.42	—	—	+.43	+.67	.	.	.	.	.	.	.	.
Spruce hybrid index	21	-.43	—	+.38	—	—	+.58	+.68	—	—	—	—	+.65	+.51	—	—	—	—	+.42	+.63	+.68	.	.	.	.	.	.	.
Fir hybrid index	22	-.67	+.49	—	-.68	-.43	—	+.41	—	—	—	—	+.67	+.37	—	-.43	—	—	+.37	+.57	+.45	+.44	.	.	.	.	.	.
L-H horizon pH	23	+.65	—	—	+.54	+.67	-.52	-.59	+.60	+.42	—	—	+.60	-.36	—	+.56	—	—	—	-.62	-.69	-.58	-.53	.	.	.	.	.
L-H horizon available Ca	24	+.46	—	—	—	+.68	—	-.45	+.80	+.40	—	—	—	—	—	+.39	—	—	—	-.36	-.46	—	—	+.71	.	.	.	.
L-H horizon TEC	25	—	—	—	—	+.67	—	-.38	+.67	—	—	—	+.36	—	—	—	+.39	—	—	—	-.37	—	—	+.45	+.78	.	.	.
A horizon pH	26	+.45	—	—	+.45	+.47	-.36	-.44	+.46	—	—	—	—	—	—	—	—	—	—	—	-.40	—	—	+.57	+.59	+.36	.	.
B horizon available Ca	27	—	—	—	—	+.42	—	-.41	+.49	—	—	—	—	—	—	—	—	—	—	-.38	-.38	—	-.37	+.63	+.63	+.45	+.67	.
C horizon available Ca	28	+.54	-.38	—	—	—	-.36	-.45	—	—	—	—	-.44	—	+.45	—	—	—	—	-.59	—	—	-.48	—	+.39	—	+.49	+.60

There was a great deal of similarity in the soils sampled and very few of the soil variables showed significant relationships with vegetational characteristics. Three reasons may be suggested. First, simple correlation assumes a linear relationship between the two variables. Other workers (e.g. Beil 1966, Stringer and La Roi 1970) have found the relationships between vegetational and soil variables to be non-linear. Consequently, simple correlation analysis may be inappropriate to express the relationship of some of the variables. Secondly, the methods used provided limited chronological and spatial sampling of the soil variability in each stand. Anderson and Tiedemann (1970) found significant differences between sampling dates for pH, total exchange capacity, and exchangeable Na, K, and Ca, while spatial variation in forest soil chemical properties has been reported by Zinke (1962) and Gersper and Holowaychuk (1971). The use of composite samples of the L-H and A horizons provided a better sampling of the spatial variation of these horizons than for the B and C horizons which were sampled by only one pit per stand. Of the six soil variables discussed below which did show good correlation with vegetational variables, four were L-H or A horizon characteristics. Thus, sampling of soil variability may have been inadequate. Thirdly, the results may be a real phenomenon which may be interpreted to mean that more properties of the L-H and A horizons are significantly related to vegetational variables than those of the B and C horizons.

Little correspondence between soil type and community type was apparent. One reason for this may be that the soil subgroup level is a relatively broadly defined unit with much internal variation. Classifi-

cation of the soils to a lower level, e.g. soil series, may show relationships better. A second reason may be that the soil classification system is based largely on visual morphological features. It appears that in general the features emphasized in soil classification to the subgroup level are not important in determining vegetation pattern. Similar conclusions have been reached by other workers (Heringa and Cormack 1963, Daubenmire and Daubenmire 1968, Daubenmire 1970).

L-H pH, L-H exchangeable Ca, L-H total exchange capacity, A pH, B exchangeable Ca, and C exchangeable Ca showed a good correlation with both vegetational variables and each other (Table 11, Figure 13). These soil variables show a gradient from higher soil nutrient levels (higher pH and exchangeable cation values) in the lower right of the field (Viburnum/Hylocomium community type), to lower soil nutrient levels to the upper left (Rubus pedatus/Ptilium community type).

In summary, the Rubus pedatus/Ptilium community type was associated with higher precipitation, cooler temperatures, and a lower soil nutrient status than the Viburnum/Hylocomium community type which was conversely drier and warmer with richer soils. The other two community types were generally intermediate in both altitude and soil fertility values.

Figure 13. Soil variables on the ordination field.

a. L-H horizon pH: 1 = < 4.0, 2 = > 4.0.

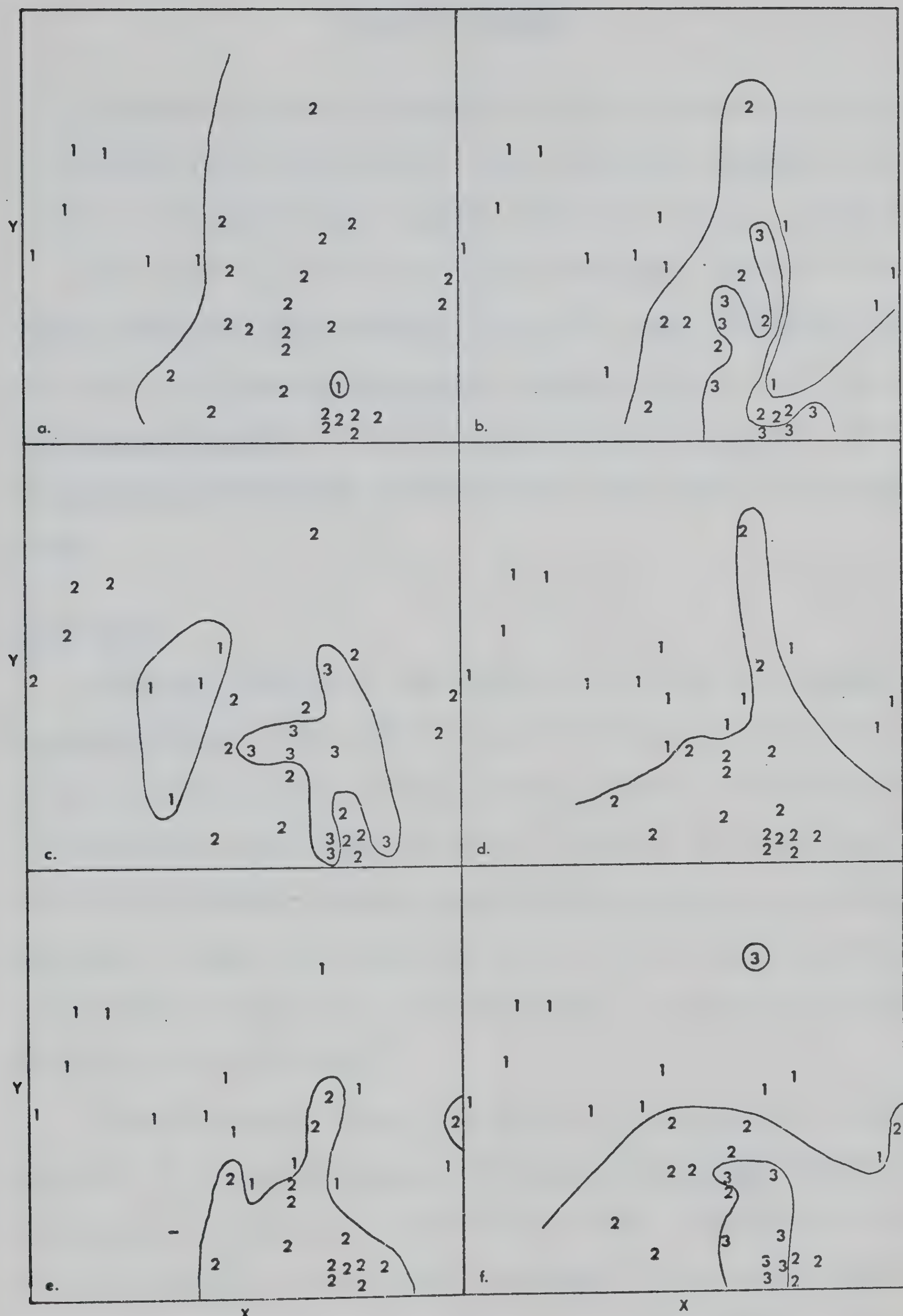
b. L-H horizon exchangeable Ca (meq/100g): 1 = < 30, 2 = 30 - 60, 3 = > 60.

c. L-H horizon total exchange capacity (meq/100g): 1 = < 40, 2 = 40 - 90, 3 = > 90.

d. A horizon pH: 1 = ≤ 4, 2 = > 4.

e. B horizon exchangeable Ca (meq/100 g): 1 = < 10, 2 = > 10.

f. C horizon exchangeable Ca (meq/100 g): 1 = < 14, 2 = 14 - 20, 3 = > 20.


a.
b.
c.
d.
e.
f.
Y
X

COMMUNITY PATTERN

Community pattern was assessed by plotting vegetational variables on the ordination field and by simple correlation analysis. The behavior of all species was examined, but only a few are considered here.

The overall pattern of the stands themselves (Figure 5) showed the *Rubus pedatus/Ptilium* community type in the upper left-hand portion of the field; the *Viburnum/Hylocomium* community type in the lower center; the *Cornus-Linnaea* community type primarily in the center; and the *Calamagrostis canadensis* community type to the right of the ordination field.

Tree Layer

Stand age (Figure 14) was oldest to the left, in the *Rubus pedatus/Ptilium* community type, and decreased to the right of the field. The pattern is very similar to that of stand altitude (Figure 12) and the two are highly correlated ($r = +0.67$, $P < 0.01$). As noted above, generally with increasing altitude precipitation increases and temperature decreases. Thus, the probability of fire would seem to decrease with increasing altitude, and a stand would have a greater probability of surviving to an older age.

Total tree cover (Figure 14) peaked in the middle of the X-axis in portions of the *Cornus-Linnaea* and *Viburnum/Hylocomium* community types. This pattern is similar to that of L-H horizon available Ca (Figure 13). The two variables are positively correlated ($r = +0.39$, $P < 0.05$) suggesting a causal relationship. Total tree density (Figure 14) reached

Figure 14. Tree layer variables on the ordination field.

a. Stand age (yrs.): 1 = <100, 2 = 100 - 149, 3 = 150 - 200, 4 = >200. Actual values in Table 13.

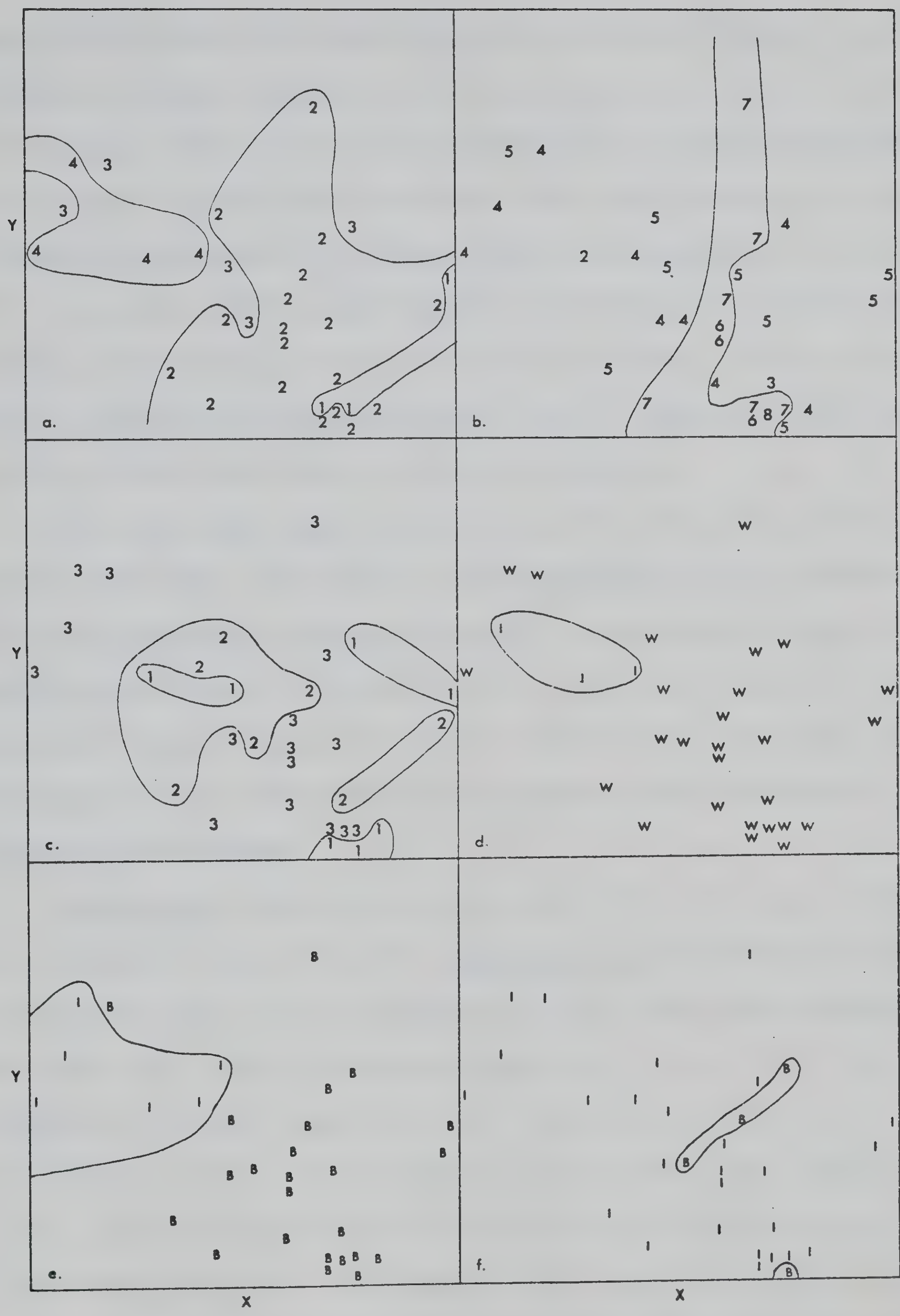
b. Total tree cover: 1 = 1 - 9%, 2 = 10 - 19%, etc.

c. Total tree density (stems/ha): 1 = <600, 2 = 600 - 700, 3 = >700.

d. Spruce morphological index: I = Intermediate, W = *Picea glauca*. Actual values in Table 7.

e. Fir morphological index: I = Intermediate, B = *Abies balsamea*, - = absent. Actual values in Table 7.

f. Geographic Index: I = Intermediate, B = Boreal. Actual values in Table 8.


a.
b.
c.
d.
e.
f.
Y
X

peaks in the center and upper left of the field with minima to the left center and right. The pattern shows some similarity to that of total tree cover. The similarity is confirmed by the significant correlation ($r = +0.54$, $P < 0.01$) between the two. Total tree density is not significantly correlated with the L-H horizon exchangeable Ca ($r = +0.15$).

The spruce and fir morphological index (Figure 14) reached maximum values (Intermediate) to the upper left of the field, primarily in the *Rubus pedatus*/*Ptilium* community type. The two indexes were well correlated with each other and with altitude (Table 11).

The four stands rated Boreal with the Geographic Index (Figure 14) were to the right of the field in the *Viburnum*/*Hylocomium* (Stands 2 and 3) and *Calamagrostis canadensis* (Stands 1 and 4) community types. The widespread occurrence of lodgepole pine accounts for the greatly expanded area occupied by the Intermediate category of the Geographic Index in comparison with the Intermediate category of the spruce and fir morphological indexes.

Picea glauca cover (Figure 15) peaked to the lower right and was at a minimum to the upper left. *Abies balsamea* cover (Figure 15) showed an inverse pattern, with a minimum to the lower right and a maximum to the upper left. This complementary patterning is confirmed by the negative correlation between the cover values of the two species ($r = -0.70$, $P < 0.01$). The pattern of spruce and fir cover closely follows that of stand altitude (Figure 12) and the correlations are significant (Table 12). Fir appears better adapted to moister, cooler, higher altitudinal situations with spruce doing better in comparatively drier, warmer, lower altitudinal situations. Similar observations on

the adaptation of these two species have been made by Rowe (1961) and Bakuzis and Hansen (1965).

Pinus contorta cover (Figure 15) peaked to the left of the field, while *Betula papyrifera* s.l. cover (Figure 15) peaked to the right. *Populus tremuloides* cover (Figure 15) showed a maximum down the middle with decreasing values to the sides in a pattern similar to that of total tree cover (Figure 14).

The distribution and abundance patterns of the tree species on the ordination are considered to depend on the tolerance ranges of the species. Although the tolerance ranges, and thus the distributions of the trees overlap, each species achieves maximum cover in a different part of the ordination field. This distribution on the ordination, based on vegetational data, is thought to represent both vegetational-physical environmental relationships and interspecific competitive relationships. These relationships are considered to define an ecological optimum or adaptive peak (Whittaker 1967) in which the species population achieves its maximum performance.

The distribution of both the community types and the understory species on the ordination reflect, to a large degree, the distribution and influence of the dominant tree species.

Shrub Layer

Total shrub cover (including tree transgressives and saplings) peaked in the center of the field (Figure 15) but otherwise showed no well-defined pattern. *Viburnum edule* cover and *Rosa acicularis* cover (Figure 16) were both maximum in the center of the field and were well

Figure 15. Tree species cover and total shrub cover on the ordination field. Actual values in Table 9.

a. <u>Picea glauca</u> cover: 1 = < 20%, 2 = 20 - 49%, 3 = ≥ 50%.

b. <u>Abies balsamea</u> cover: 1 = < 10%, 2 = 10 - 30%, 3 = > 30%, - = absent.

c. <u>Pinus contorta</u> cover: 1 = < 15%, 2 = > 15%, - = absent.

d. <u>Betula papyrifera</u> s.l. cover: 1 = < 5%, 2 = > 5%, - = absent.

e. <u>Populus tremuloides</u> cover: 1 = ≤ 5%, 2 = > 5%, - = absent.

f. Total shrub cover: 1 = 1 - 9%, 2 = 10 - 19%, etc.


a.
b.
c.
d.
e.
f.
Y
Y
Y
X
X

Figure 16. Shrub species cover on the ordination field. Actual values in Table 9.

a. Viburnum edule cover: 1 = < 10%, 2 = ≥ 10%, - = absent.

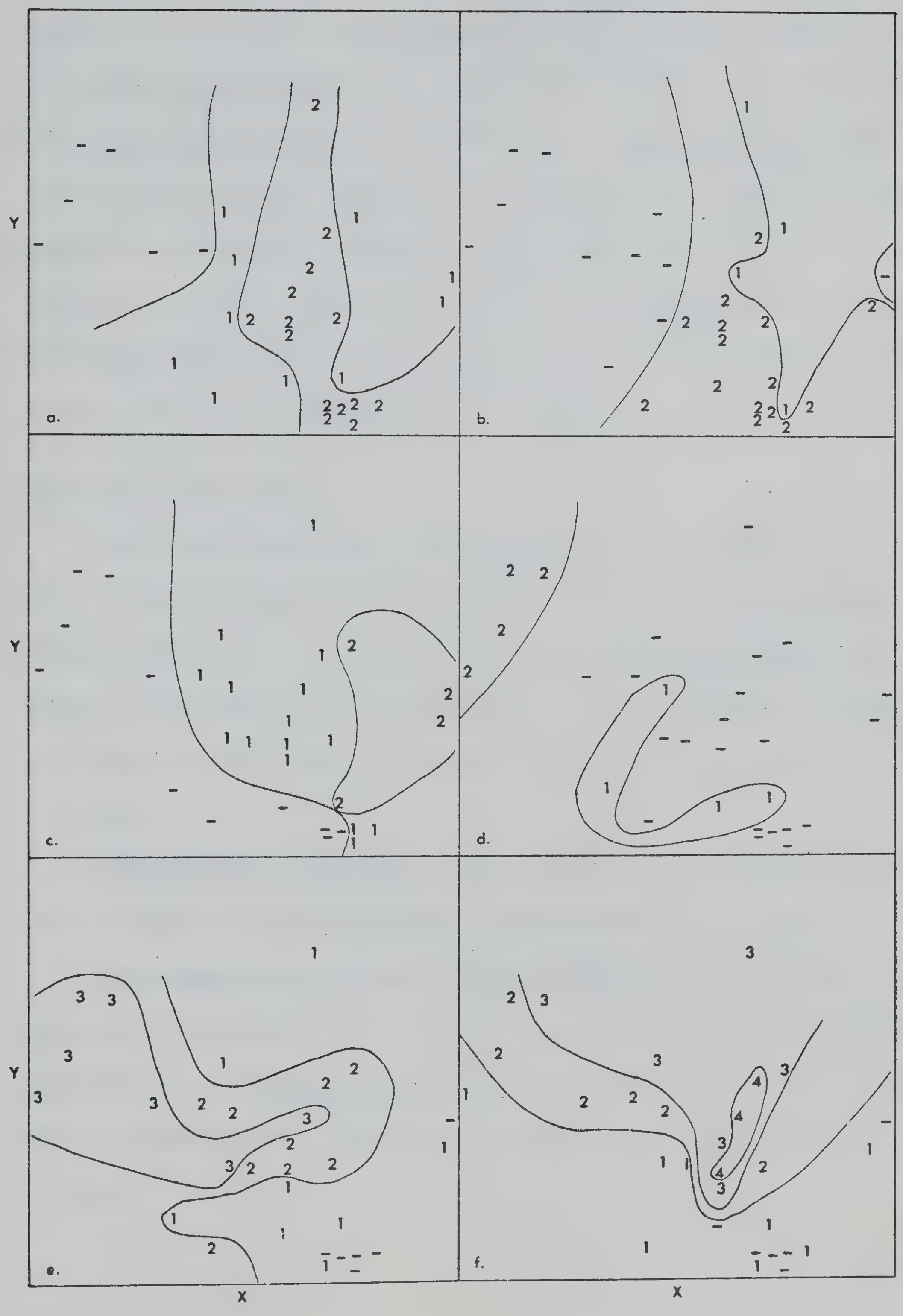
b. Rosa acicularis cover: 1 = ≤ 1%, 2 = > 1%, - = absent.

c. Rubus strigosus cover: 1 = < 5%, 2 = > 5%, - = absent.

d. Ledum groenlandicum cover: 1 = < 1%, 2 = > 1%, - = absent.

e. Abies balsamea transgressives: 1 = < 5%, 2 = 5 - 9%, 3 = ≥ 10%, - = absent.

f. Abies balsamea saplings: 1 = < 5%, 2 = 5 - 10%, 3 = 11 - 19%, 4 = ≥ 20%, - = absent.


a.
b.
c.
d.
e.
f.
Y
Y
Y
X
X

correlated ($r = +0.59$, $P < 0.01$). *Rubus strigosus* cover (Figure 16) was highest to the right in the *Calamagrostis canadensis* community type, and *Ledum groenlandicum* cover (Figure 16) peaked to the upper left in the *Rubus pedatus*/*Ptilium* community type. *Abies balsamea* sapling cover (Figure 16) was highest in the center of the field and decreased outwards, while *Abies balsamea* transgressive cover (Figure 16) was highest at the left margin of the field and decreased to the right. Both *Picea glauca* transgressive and sapling cover (Figure 17) peaked in the center and decreased to the margins.

Herb-Dwarf Shrub Layer

Total herb-dwarf shrub cover (Figure 17) was highest to the right of the field and generally decreased to the left. *Rubus pedatus* cover (Figure 17) peaked to the upper left, while *Rubus pubescens* cover (Figure 17) peaked to the lower right. The two species overlapped in the center of the field, but generally did not occur together ($r = -0.46$, $P < 0.01$).

Calamagrostis canadensis cover (Figure 17) was maximum to the right of the field in the *Calamagrostis canadensis* community type.

Both *Linnaea borealis* and *Cornus canadensis* cover (Figure 18) were highest in the center of the field where the species were understory dominants in the *Cornus*-*Linnaea* community type. Mean cover values for the two species were highly significantly correlated ($r = +0.55$, $P < 0.01$).

Figure 17. Shrub and herb-dwarf shrub species cover on the ordination field. Actual values in Table 9.

a. _Picea glauca_ sapling cover: 1 = $\leq$ 1%, 2 = > 1%, - = absent.

b. _Picea glauca_ transgressive cover: 1 = < 1%, 2 = $\geq$ 1%, - = absent.

c. Total herb-dwarf shrub cover: 1 = 1 -9%, 2 = 10 - 19%, etc.

d. _Rubus pedatus_ cover: 1 = < 15%, 2 = > 15%, - = absent.

e. _Rubus pubescens_ cover: 1 = present - = absent.

f. _Calamagrostis canadensis_ cover: 1 = < 20%, 2 = > 20%, - = absent.

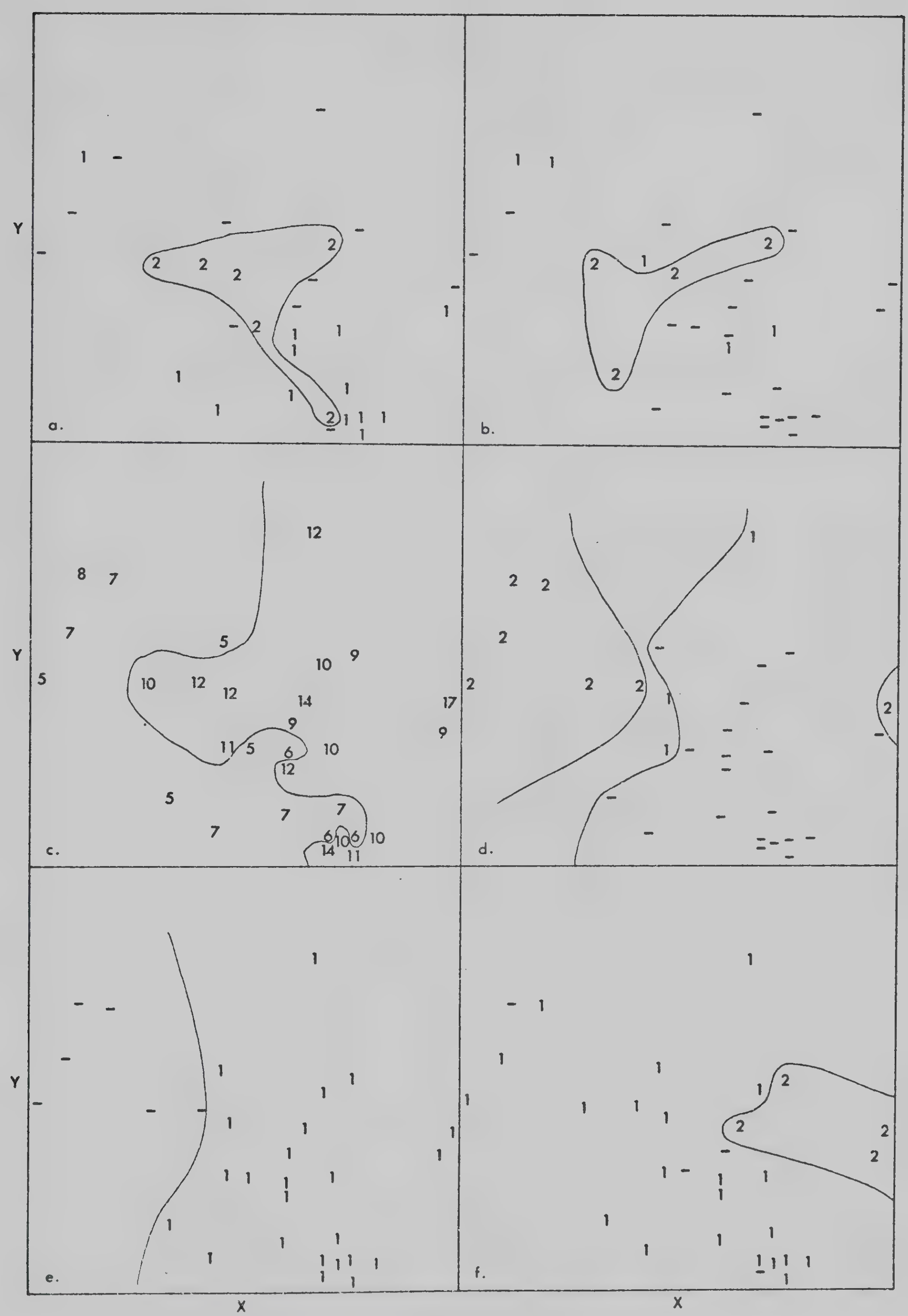

a.
b.
c.
d.
e.
f.
Y
X

Figure 18. Herb-dwarf shrub and bryoid species cover on the ordination field. Actual values in Table 9.

a. *Linnaea borealis* cover: 1 = $\leq$ 12%, 2 = > 12%
- = absent.

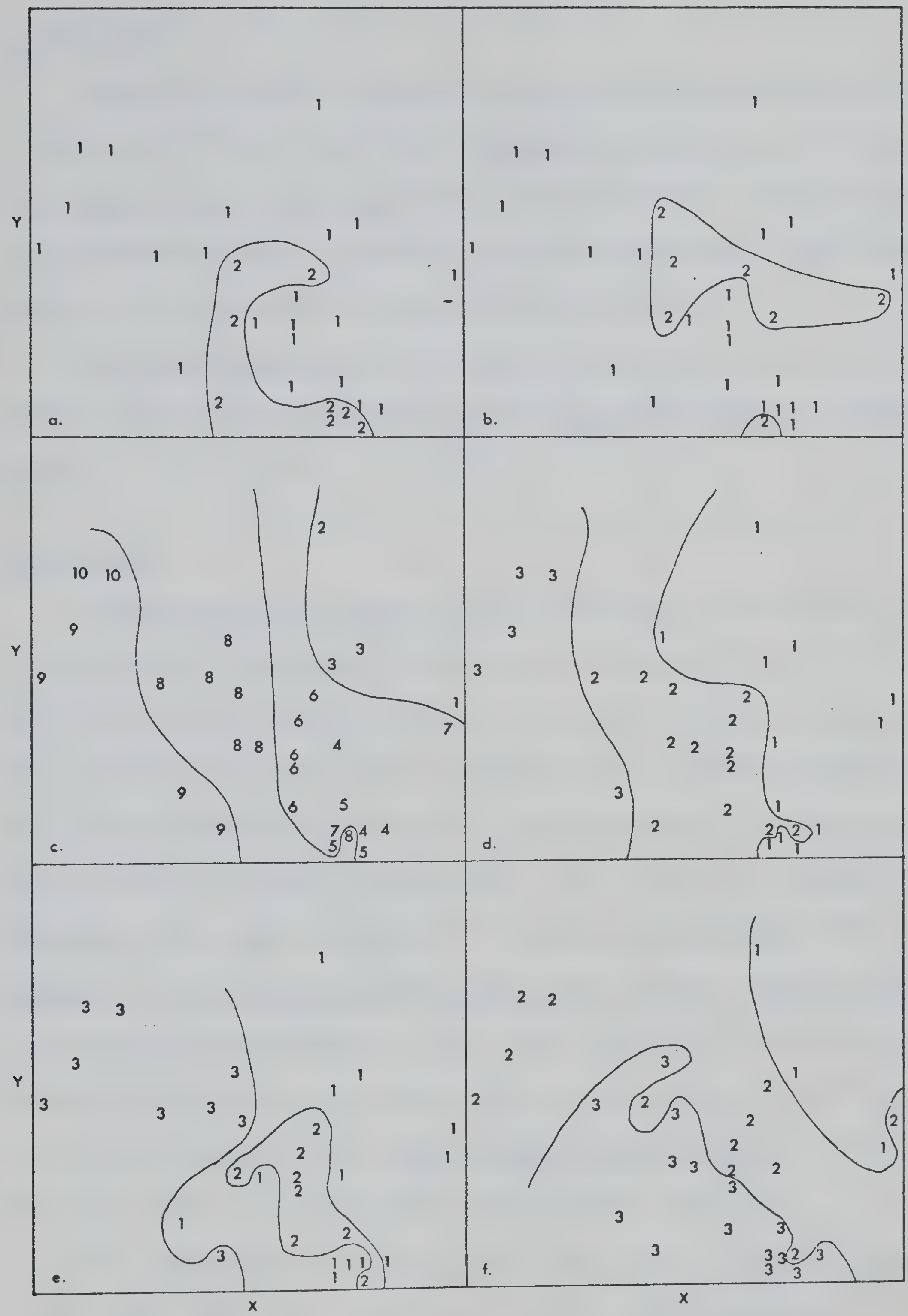
b. *Cornus canadensis* cover: 1 = < 20%, 2 = $\geq$ 20%.

c. Total bryoid cover: 1 = 1 - 9%, 2 = 10 - 19%, etc.

d. *Pleurozium schreberi* cover: 1 = $\leq$ 10%, 2 = 11 - 30%, 3 = > 30%.

e. *Ptilium crista-castrensis* cover: 1 = < 10%, 2 = 10 - 25%, 3 = >25%.

f. *Hylocomium splendens* cover: 1 = < 10%, 2 = 10 - 30%, 3 = > 30%.


a.
b.
c.
d.
e.
f.
Y
X

Bryoid Layer

Total bryoid cover (Figure 18) showed a strong gradient from high at the left to low at the right. Pleurozium schreberi cover (Figure 18) and Ptilium crista-castrensis cover (Figure 18) were patterned similarly ($r = +0.61$, $P < 0.01$) and both were well correlated with total bryoid cover ($r = +0.76$ and $+0.73$ respectively, $P < 0.01$).

Hylocomium splendens cover (Figure 18) was highest in the lower portion of the field primarily in the Viburnum/Hylocomium community type.

Conclusions

Similarities can be seen in the distribution and abundance patterns of many of the vegetational variables on the ordination field. Variables with similar patterns also tend to be positively correlated (Table 11). Two groups of vegetational variables are largely correlated (Table 11) with the altitudinal and soil fertility gradients recognized in the Environmental Relations section above. The first group includes: Abies balsamea cover, Pinus contorta cover, Ledum groenlandicum cover, Rubus pedatus cover, Vaccinium membranaceum cover, Ptilium crista-castrensis cover, Pleurozium schreberi cover, total bryoid cover, stand age, and both spruce and fir morphological index values. This group of variables corresponds largely to the Rubus pedatus/Ptilium community type and is associated with higher altitudes and lower soil fertility.

The second group includes: Picea glauca cover, Populus tremuloides cover, total tree cover, total tree density, Viburnum edule cover, Rosa acicularis cover, total shrub cover, Rubus pubescens cover, Linnaea

borealis cover, and Hylocomium splendens cover, corresponds largely to the Viburnum/Hylocomium community type, and is associated with lower altitudes and higher soil fertility levels.

The existence of these two groups of variables strengthens the conclusions drawn earlier about the relationships of the community types. The basically coniferous Rubus pedatus/Ptilium and the mixed-wood Viburnum/Hylocomium community types are the main types described here. The Cornus-Linnaea community type is intermediate between these two, and the Calamagrostis canadensis community type shows similarities to both the Cornus-Linnaea and Viburnum/Hylocomium community types.

In examining the relationships of the environmental and vegetational variables several problems arise. The first is that the use of simple correlation analysis (Table 11) assumes a linear relationship between the variables. Other workers (e.g. Beil 1966, Stringer and La Roi 1970) have found the relationships to be frequently non-linear. Thus the use of non-linear methods may show significant relationships not discovered here. The use of multiple regression analysis, which considers the simultaneous effect of other variables, may be helpful.

The second problem concerns the use and interpretation of moisture and soil fertility levels. The physiological requirements for these factors by the species involved are not known. Neither is it possible to estimate the role of factor interaction and factor compensation. Thus it is not possible to say if any of the factors considered here are actually limiting. Causality is often inferred from significant correlation, but should not be assumed to be proved by it.

A third problem concerns the environmental data used. The soils data were collected from only one pit per stand which provided a very limited sampling of spatial and chronological soil variability in each stand, as discussed on page 72. Moisture conditions were inferred from temperature and precipitation data collected often some distance from the stand, rather than being based on actual soil moisture measurements in each stand.

Thus, the relationships indicated in the Environmental Relations and Community Pattern sections must be considered as only tentative.

GEOGRAPHIC RELATIONS

Floristics

The flora of the study area is basically of boreal affinity, but also contains distinctive cordilleran and Pacific elements (Moss and Pegg 1963). Several of these cordilleran and Pacific species reach their eastern limits in central Alberta spruce-fir forests, particularly in Swan Hills.

Plants of primarily cordilleran affinity (Moss and Pegg 1963) found in the spruce-fir stands studied were: *Abies lasiocarpa*, *Arnica cordifolia*, *Dryopteris assimilis*, *Menziesia glabella*, *Picea engelmannii*, *Pinus contorta* var. *latifolia*, *Rhododendron albiflorum*, *Rubus pedatus*, *Sorbus scopulina*, and *Vaccinium membranaceum*. Species of basically Pacific affinity which occurred in the study stands were *Oplopanax horridum* and *Tiarella trifoliata*.

Table 12 shows the occurrence of the cordilleran and Pacific elements by community type. The *Rubus pedatus*/*Ptilium* community type has the greatest number of occurrences of the "western" floristic elements, and the *Viburnum*/*Hylocomium* community type has the fewest.

Forest Sections

Rowe (1959) separated the Lower Foothills Section (B19a) of the Boreal Region from the Mixedwood (B18a) and Hay River (B18b) Sections largely on the basis of ". . . the appearance of Cordilleran forest elements, particularly lodgepole pine. . . . The distinctive tree species [for the Lower Foothills Section] is the lodgepole pine." Three eastern outliers of the Lower Foothills Section were identified

Table 12. Occurrence of cordilleran and Pacific floristic elements by community type.

Species	Community type: Rubus pedatus/ Ptilium	Cornus-Linnaea	Viburnum/ Hylocomium	Calamagrostis canadensis
Abies lasiocarpa	X			
Arnica cordifolia	X	X	X	X
Dryopteris assimilis	X	X	X	X
Menziesia glabella	X			
Picea engelmannii	X			
Pinus contorta	X	X	X	X
Rhododendron albiflorum	X			
Rubus pedatus	X	X		X
Sorbus scopulina	X	X	X	X
Vaccinium membranaceum	X			
Oplopanax horridum	X	X		X
Tiarella trifoliata	X			
Number of occurrences	12	6	4	6

by Rowe: the Caribou Mountains and Marten Mountain-Pelican Mountain in northern Alberta (Figure 1), and the Cypress Hills in southeastern Alberta and southwestern Saskatchewan.

This study has identified an additional area, Watt Mountain (Figure 1), as a small outlier of the Lower Foothills Section in northwestern Alberta.

The Christina highland (Figure 1) is best left in the Mixedwood Section (Rowe 1959). Although the pine populations were predominantly lodgepole, the stands were rated as Boreal on the Geographic Index (Table 8), and the floristic affinities of the other species are primarily boreal.

Two other northern highland areas, the Birch Mountains and the Buffalohead Hills (Figure 1), were not investigated. Raup (1933) and Critchfield and Little (1966) have reported cordilleran floristic elements from these areas which suggests that they should perhaps be included in the Lower Foothills Section. However, present information is insufficient to make such a decision.

Comparison with other studies

In the following discussion the term "similarity" is frequently used or implied. The lack of suitable published data has not permitted a quantitative analysis of similarity among the various vegetation types discussed, and thus similarity has been judged, somewhat subjectively, on the basis of floristic composition and dominance.

In addition, few workers have described the bryophyte and lichen component of the vegetation in their study areas. This makes comparison

with the results of this study more difficult since the bryophytes and lichens are an important part of the vegetation of spruce-fir forests and have played an important role in the recognition of community types in this study.

The forest descriptions of Raup (1933, 1934, 1946) and Moss (1953, 1955, Moss and Pegg 1963) are primarily floristic and non-quantitative and it is difficult to relate them to the community types recognized here.

Raup (1933, 1934, 1946), working primarily in northern Alberta, used the category "upland spruce forests" which is much broader than the community type and which he did not divide into smaller categories. All of the stands in the present study were upland spruce forests by virtue of the stand selection criteria. Many of the species listed by Raup were found in the present study.

In a series of papers, Moss (1953, 1955, Moss and Pegg 1963) divided upland spruce forest in northern Alberta into several Clementsian associations and faciations. The "shrub-herb faciation" of the "white spruce association" (Moss 1953) is very similar to the *Viburnum/Hylocomium* community type. The "grass-shrub faciation" (Moss 1953), characterized by *Elymus innovatus* and *Shepherdia canadensis* on dry sites, has no counterpart here.

The "feather moss faciation", which Moss (1953) likens to Raup's upland spruce forests, occurs under a dense tree canopy and floristically is closest to the *Viburnum/Hylocomium* community type. However, the classification is somewhat confusing in that the "feather moss faciation" is later equated with the "white spruce association" of the

"boreal-cordilleran transition forests" (Moss 1955), and with the "white spruce faciation" of the "upland coniferous forest" (no association indicated) (Moss and Pegg 1963).

La Roi (1967), using qualitative floristic criteria, recognized a white spruce-fir, Populus/Salix/Shepherdia, Lonicera/Rubus-Lathyrus stand-group in northwestern Alberta and adjacent Mackenzie District, N.W.T. The stand-group is based on quite different criteria from those used in the present study and is a broader unit than the community type. However it is a mixedwood type and as such is similar to the Viburnum/Hylocomium community type. In the white spruce-fir stands, the Lower Foothills Section was represented by a stand which, based on the quantitative data given, would fit into the Viburnum/Hylocomium community type.

Working in the Lower Foothills Section in central Alberta, Lesko and Lindsay (1973) described four white spruce associations: the white spruce-horsetail (Equisetum arvense) association, the white spruce-sarsaparilla (Aralia nudicaulis) association, the white spruce-feather moss (Hylocomium splendens) association, and the white spruce-blueberry (Vaccinium myrtilloides) association. The classification methodology was Zurich-Montpellier and the associations do not correspond entirely to any of the four community types. For example, Dryopteris dilatata and Lycopodium obscurum, the "exclusive" species for the white spruce-sarsaparilla association, occur in four and three of the community types, respectively. From the qualitative listing of character, constant, and companion species, the four associations appear most like the Viburnum/Hylocomium community type.

Duffy (1965) recognized five communities in the Mixedwood Section of Alberta. His shrub-herb-moss community, which occurs characteristically on moderately well-drained sites, is very similar to the *Viburnum*/*Hylocomium* community type. The other four communities have no counterpart here.

Plochmann (1956) recognized a spruce-poplar-fir type (*Picea glauca*-*Populus balsamifera*-*Abies balsamea*) as the climax type on mineral soils in northwestern Alberta. This broad category seems equivalent to Raup's "upland spruce forests." Only tree data were presented but many of the stands appear to be close to the *Viburnum*/*Hylocomium* community type.

Newsome and Dix (1968) described the forests of the Cypress Hills which are a southeastern outlier of the Lower Foothills Section. No *Abies* occurs in the Cypress Hills, but the white spruce forests are similar to those in northern Alberta. The white spruce-aspen forest shows greatest affinity to the *Viburnum*/*Hylocomium* community type. The white spruce-lodgepole pine forest contains a combination of species unlike any of the community types recognized here. This coniferous forest appears to be much drier than the nearly pure conifer *Rubus pedatus*/*Ptilium* community type in northern Alberta.

To the east of the study area, Halliday (1929, 1930) delineated forest types in Manitoba and Saskatchewan. The Herb type of Grass-Herb Forest and the Transition type of Moist Moss Forest appear most similar to the *Viburnum*/*Hylocomium* community type. The *Hylocomium* type of Moist Moss Forest is perhaps closest to the *Viburnum*/*Hylocomium* community type.

In Manitoba and Saskatchewan, Rowe (1956) described the forest vegetation of a region very similar floristically to northern Alberta. The Picea-Populus/Calamagrostis-Aster-Anemone community closely resembles the Calamagrostis canadensis community type. The Picea/Mitella-Petasites-Mertensia community, the Picea-Abies/Hylocomium-Viola-Trientalis community, and the Picea/Cornus-Linnaea-Vaccinium community are all similar to the Viburnum/Hylocomium community type. The stands with a nearly pure conifer canopy and well developed moss layer, are perhaps structurally similar to the Rubus pedatus/Ptilium community type, but are quite different floristically containing elements more typical of the Viburnum/Hylocomium community type.

Van Groenewoud (1965a) analyzed white spruce communities in central Saskatchewan using both vegetational and soil characteristics. Chi-square association analysis was used to recognize three community types. The Equisetum pratense and E. arvense community types appear unlike any of the community types recognized here although the lack of vegetational data makes comparison difficult. Equisetum pratense did not occur in any of the stands studied, while E. arvense occurred sporadically, primarily in the Viburnum/Hylocomium type. The third community type, "a very variable community type typified by a more-or-less developed moss-herb--shrub vegetation" (van Groenewoud 1965a), was subsequently classified (van Groenewoud 1965b) by the Zurich-Montpellier method into three vegetation units. The three units most closely resemble the Viburnum/Hylocomium community type. However, van Groenewoud's vegetation data (1965b) show only Viburnum trilobum and not V. edule which was the dominant shrub in northern Alberta. It appears that a

misidentification has been made since Swan and Dix (1966, Dix and Swan 1971) working in the same area of central Saskatchewan, reported V. edule from white spruce forests, but did not list V. trilobum.

Swan and Dix (1966, Dix and Swan 1971) studied upland forests in the Mixedwood Section of central Saskatchewan. Their Picea glauca dominated stands resemble those of the Viburnum/Hylocomium community type. Their Abies balsamea dominated stands are also closest to those of the Viburnum/Hylocomium community type, whereas northern Alberta stands with large amounts of Abies balsamea generally were classified as either the Rubus pedatus/Ptilium or Cornus-Linnaea community type.

Horton (1959) studied forests immediately west of the study area in the Upper Foothills Section and the East Slope Rockies Section (Rowe 1959). This region is in the western portion of the transition from boreal to cordilleran forests. The spruce populations ranged from Picea glauca in the valleys, through "a complex gradient resembling a hybrid swarm" (Horton 1959) on the lower and mid-slopes, to P. engelmannii above 1830 m. Horton divided the communities into Picea glauca, Intermediate and P. engelmannii types based on a hybrid index evaluation. The Picea glauca type is closest to the Viburnum/Hylocomium community type. Although aspen appears to be absent, the small amount of fir, the predominance of boreal species in the understory, and the hybrid index determination of Picea glauca, all suggest such affinity.

The Picea engelmannii type contained an abundance of fir and cordilleran elements such as Menziesia glabella and Vaccinium membran-

aceum which suggest a similarity to the Rubus pedatus/Ptilium community type. However, Rubus pedatus was apparently absent in all types. The Intermediate type appears similar to the Cornus-Linnaea community type.

The cordilleran sub-alpine spruce-fir forests to the west and south of the study area are structurally similar to those of the study area, but show weaker floristic affinities than do the boreal spruce-fir forests to the east.

Beil (1966) described sub-alpine spruce-fir forests in Jasper and Banff National Parks. The spruce were considered to be "a hybrid swarm of intermediates. . . inclined toward Engelmann spruce." Using presence of herb and dwarf shrub species, Beil showed that the Jasper and Banff spruce-fir forests had greater floristic affinity to boreal spruce-fir forests west of Lake Winnipeg than to cordilleran spruce-fir forests described by Oosting and Reed (1952) in southern Wyoming. However, a geographic floristic gradient was apparent in Beil's data and the more southern stands showed greater cordilleran affinities. Stands in Jasper and northern Banff (north of Bow Pass) at altitudes of 1675 to 1920 m contained Rubus pedatus and are similar to the Rubus pedatus/Ptilium community type.

Ogilvie (no date a & b, 1960, 1963, Kirby and Ogilvie 1969) studied the sub-alpine forests around Banff National Park. The Picea-Abies/Menziesia-Lycopodium habitat type was widespread and is most similar to the Rubus pedatus/Ptilium community type. The Picea-Abies/Hylocomium-Cornus habitat type occurred on warmer, drier sites within the Picea-Abies/Menziesia-Lycopodium habitat type and resembles the Cornus-Linnaea community type.

Ogilvie (1962) pointed out a floristic discontinuity at about 50° N in southwestern Alberta. Descriptions of spruce-fir forests south of this boundary in southwestern Alberta (Kuchar 1973), Montana (Kirkwood 1922, Patten 1963, Habeck 1967), northern Idaho and eastern Washington (Daubenmire and Daubenmire 1968), Wyoming (Blake 1945, Oosting and Reed 1952, Despain 1971), and Colorado (Stahelin 1943, Langenheim 1962), indicate that the affinity of these forests with those in the study area is not strong. While there is marked structural similarity, the vascular understory plants, in particular, are quite different.

Arlidge (Illingworth and Arlidge 1960) described site types in *Picea glauca*-*Abies lasiocarpa* forests around Prince George, B.C. Both the *Cornus*-Moss and the *Aralia*-*Dryopteris* site types have major similarities to the *Cornus*-*Linnaea* community type and lesser ones with the *Rubus pedatus*/*Ptilium* community type.

Kujala (1945) delineated forest vegetation types for much of British Columbia and portions of the adjacent Rocky Mountains in Alberta. The *Rubus pedatus*/*Ptilium* community type corresponds most closely to his *Tiarella*-*Rubus pedatus* sub-type, and has somewhat lesser affinities to the *Tiarella*-*Rubus pedatus*-*Rhododendron* sub-type. The *Rubus pedatus*-*Vaccinium membranaceum* sub-type resembles the *Cornus*-*Linnaea* community type, and the *Mitella*-*Cornus* sub-type shows relationships with both the *Cornus*-*Linnaea* and *Viburnum*/*Hylocomium* community types.

Revel (1968), in a study of the Sub-boreal Spruce Zone (Krajina 1965) of northern British Columbia, recognized a Picea glauca-Populus tremuloides-Alnus sinuata-Aralia nudicaulis-Moss (Ptilium crista-castrensis, Hylocomium splendens, Pleurozium schreberi) association which resembles the Viburnum/Hylocomium community type recognized here. The Picea glauca-Abies lasiocarpa-Rubus pedatus-Cornus canadensis-Moss (Ptilium crista-castrensis, Pleurozium schreberi) association appears closest to the Rubus pedatus/Ptilium community type.

To the north, in the southwestern part of the Northwest Territories, Raup (1947) briefly described upland spruce forests. In the vicinity of Fort Simpson, these forests are generally comparable to the upland spruce forests of northern Alberta (Raup 1933, 1934, 1946), which were previously discussed. The Fort Simpson forests show strong boreal floristic affinities, and are most similar to the Viburnum/Hylocomium community type. The white spruce forests further to the west, near the Yukon Territory border, do not appear similar to any of the community types recognized in the present study.

Jeffrey (1964) also worked in the southwestern Northwest Territories, and recognized a series of forest types. The mixed coniferous (high elevation) and the alpine fir forest types of the Mackenzie Mountains, both show affinities to the Rubus pedatus/Ptilium community type; the former more so than the latter. The mixed coniferous (low elevation) forest type of the Mackenzie Mountains and the mixedwood forest type of the Mackenzie lowland are both similar to the Viburnum/Hylocomium community type.

Lutz (1956) described broadly-defined forest types from the interior of Alaska. His Picea glauca and P. glauca-Populus tremuloides types are quite similar to the Viburnum/Hylocomium community type. His Picea glauca-Betula papyrifera type has affinities with the Calamagrostis canadensis community type. Calamagrostis canadensis is important in the understory of many of the forest types in the Alaskan interior.

Within the study area there is a significant trend (Table 12) of increasing amounts of fir and decreasing amounts of spruce with increasing altitude, which is similar to the west to east trend across North America noted by La Roi (1967). As one moves from eastern Canada into the Prairie Provinces, fir cover becomes quite low in comparison to that of spruce (Table 9, Viburnum/Hylocomium community type). Then as one moves within Alberta to higher altitudes from the mixedwood Viburnum/Hylocomium community type, through the transitional Cornus-Linnaea community type, into the Rubus pedatus/Ptilium community type, fir cover increases to amounts equal to or greater than spruce. Sambucus pubens, Listera cordata, and Coptis trifolia show a similar pattern in that they occur only in the higher altitude stands in Alberta and only in eastern Canada in La Roi's (1967) study. Thus, although the floristic differences between the boreal forest of Alberta and that of eastern Canada are large, the performance patterns of several species suggest a similarity between the Rubus pedatus/Ptilium community type and boreal spruce-fir forests of eastern Canada. Further support comes from Moss and Pegg (1963) who have noted the occurrence of several species with eastern affinities which occur in other vegetation types in the highlands of northern Alberta.

Table 13 summarizes the occurrence, by geographic area, of the vegetation types discussed above. The *Rubus pedatus*/*Ptilium* community type has its greatest affinities with the spruce-fir forests of the Far-Northern Rocky Mountains (Daubenmire 1943) of Alberta, northern British Columbia, and southwestern Northwest Territories. Cordilleran spruce-fir forests south of about 50° N are structurally similar to the forests of the study area but quite different floristically.

The *Cornus*-*Linnaea* community type also shows relationships with the cordilleran forests of Alberta and northern British Columbia and appears to be intermediate between the preceding and following community types.

The *Viburnum*/*Hylocomium* community type is related most closely to the mixedwood forests of the closed boreal forest (Hare and Ritchie 1972) which extends from Alaska to Newfoundland. The relationships have been traced only as far east as Manitoba (Halliday 1929, 1930, Rowe 1956) since the floristic differences become marked further to the east (La Roi 1967).

Forest types similar to the *Calamagrostis canadensis* community type occur in the mixedwood forests of Alaska (Lutz 1956), and Manitoba and Saskatchewan (Rowe 1956).

Table 13. Occurrence by geographic area of similar vegetation types described by other authors. See text for details.

Geographic Area	Reference		Community type: Rubus pedatus/Ptilium	Cornus-Linnaea	Viburnum-Hylocomium	Calamagrostis canadensis
Boreal Alberta	Moss	1953	-	-	x	-
	La Roi	1967	-	-	x	-
	Lesko and Lindsay	1973	-	-	x	-
	Duffy	1965	-	-	x	-
	Plochmann	1956	-	-	x	-
	Newsome and Dix	1968	-	-	x	-
Manitoba and Saskatchewan	Halliday 1929,	1930	-	-	x	-
	Rowe	1956	-	-	x	x
	van Groenewoud	1965	-	-	x	-
	Swan and Dix	1966	-	-	x	-
Rocky Mountain Alberta	Horton	1959	x	x	x	-
	Beil	1966	x	-	-	-
	Ogilvie	var. dates	x	x	-	-
Northern British Columbia	Arlidge	1960	x	x	-	-
	Kujala	1945	x	x	x	-
	Revel	1968	x	-	x	-
Northwest Territories	Raup	1947	-	-	x	-
	Jeffrey	1964	x	-	x	-
Alaska	Lutz	1956	-	-	x	x

SUCCESSION AND CLIMAX

The influence of fire on the western boreal forest has been well documented (Raup 1946; Moss 1953, 1955; Horton 1956, 1959; Lutz 1956; Rowe 1956, 1961; Scotter 1963; Jeffrey 1964; Dix and Swan 1971). As a consequence of frequent fire, stands of forest such as those investigated here comprise a very small portion of the landscape. The balance of the upland is occupied by younger, post-fire communities.

Although post-fire succession has been generally acknowledged to occur, the concept of boreal climax vegetation has been the subject of much difference of opinion. Since *Picea glauca* and *Abies balsamea* in the study area show evidence of introgression with *P. engelmannii* and *A. lasiocarpa* respectively, and since the ecologies of the two spruce and two fir species are quite similar, evidence and opinion from both cordilleran and boreal spruce-fir forests will be considered.

Spruce-fir forests have been considered a self-perpetuating, climax type by Oosting and Reed (1952), Cormack (1953), Plochmann (1956) and Beil (1966). Moss (1955) interpreted white spruce forests "as the climax vegetation on mesic sites", but also said, "it seems doubtful whether this community is self-perpetuating."

Several authors (Moss and Pegg, 1963; Daubenmire and Daubenmire 1968; Day 1972) have considered the climax forest to be dominated by fir with lesser amounts of spruce, since fir regeneration is often prominent in old stands.

However, other workers (Oosting and Reed 1952; Horton 1959; Beil 1966) have suggested that while fir reproduction is prolific, rela-

tively few develop into mature trees compared to spruce. Thus the forest will remain predominantly spruce.

Bloomberg (1950), Horton (1959), and Rowe (1961) considered the matter of climax to be largely an academic question since fire is so prevalent that a stand is not likely to remain unburned long enough for a second generation of spruce-fir canopy trees to become established. Rowe (1961) described the western boreal forest as "a disturbance forest [in which no species has] in full the silvical characteristics appropriate to participation in a self-perpetuating 'climax'. . . . Only balsam fir has the ability to consistently reproduce itself on the forest humus under a closed canopy of the longer-lived trees, but as this species is otherwise poorly adapted to the relatively dry continental interior environment its importance in the general forest picture is minor."

Dix and Swan (1971) have taken a similar position: "Any attempt to fit the vegetation into the mold of a climax concept would be unreal and, in our opinion, unjustified."

Thus opinion ranges from succession to a self-perpetuating climax forest dominated by spruce or fir, to succession without a terminal climax stage but merely a long-lived forest which tends "to remain open, unhealthy, ragged and frequently brush-filled, awaiting the rejuvenating touch of fire, flood, or windfall-ploughing of the soil" (Rowe 1961).

While climax vegetation may have been largely a matter of theoretical interest due to the prevalence of fire, increasingly effective fire control (Day 1972) may permit the development of stands for much

longer periods of time than at present.

All of the stands investigated showed evidence of fire history (*e.g.* charcoal and burn scars) and appear to be almost entirely first generation spruce or spruce and fir following fire. Horton's (1956) observation that stands more than 150 years are very rare is borne out by the ages of the stands in the *Calamagrostis canadensis*, *Viburnum/Hylocomium*, and *Cornus-Linnaea* community types (Table 14). The stands of the *Rubus pedatus/Ptilium* community type are older, suggesting a lower frequency of fire, perhaps due to higher precipitation and lower temperatures at higher elevations (Table 4).

Following fire, *Populus tremuloides* and/or *Pinus contorta* are the primary pioneer trees, although both *Picea mariana* (black spruce) and *Picea glauca* appear to seed directly into burned sites also, usually in lesser numbers. The aspen and pine have faster initial growth rates than spruce and a typical stand 40-50 years after a fire has a canopy of aspen and/or pine with spruce in the understory. Fir appears to enter a stand at around 50-75 years although this is not inevitable (see stands 5, 19, 21, 23, 27; Table 9). At about 50-75 years after fire for aspen (Moss 1932, 1955), and 70-125 years for pine (Horton 1955, 1956; Moss 1955; Day 1972), spruce overtakes the aspen and/or pine canopy and becomes dominant. With further development the pine and aspen decline, although the rate of succession varies with initial stocking rates of the species and site conditions (Horton 1956). Lodgepole pine is considerably longer lived (290 years, Horton 1956) than aspen (120 years, Moss 1932) and old pine were still present in the oldest stands studied.

Table 14. Stand Age

Community type and Stand	Years
Rubus pedatus/ Ptilium	
6	164
7	234
8	197
9	217
10	228
29	256
Mean	216
Cornus-Linnaea	
11	123
15	113
18	126
25	141
28	164
Mean	133
Viburnum/ Hylocomium	
2	159
3	137
12	116
13	116
14	123
16	110
17	120
19	87
20	101
21	125
22	111
23	65
24	135
27	108
30	115
Mean	115
Calamagrostis canadensis	
1	106
4	155
5	86
26	128
Mean	119

These successional events generally describe the apparent developmental histories of the stands studied. The *Rubus pedatus*/*Ptilium* community type appears to have developed primarily from pine-white spruce or sometimes pine-black spruce seral stages, the *Cornus-Linnaea* community type from pine-aspen-white spruce seral stages and the *Viburnum*/*Hylocomium* and *Calamagrostis canadensis* community types primarily from aspen-white spruce seral stages.

Rowe's (1956) observations on the origin of his *Picea-Populus*/*Calamagrostis-Aster-Anemone* type are germane here: "Following fires or logging *Calamagrostis canadensis* often spreads rapidly forming a meadowland type of vegetation which persists even after the forest has been re-established. . . . There is apparently little difference in the composition of the vegetation whether associated with aspen, balsam poplar or open stands of white spruce. . . . The reason may possibly be traced to the underlying heavy-textured soils which are subject to surface flooding in the spring."

Corns (1972) studied early succession following clearcutting in the western part of the Lower Foothills Section in Alberta. His finding that *Calamagrostis canadensis* formed a thick turf on the moister, altitudinally higher sites supports Rowe's hypothesis concerning soil moisture. Corns also found that a dense *Calamagrostis* sward reduced tree regeneration establishment which may explain the low tree density noted both by Rowe and in the present study.

Lutz's (1956) stands with a *Calamagrostis* dominated understory were certainly of fire origin and although no statements about soil moisture were made, it can be inferred from the species listed that the

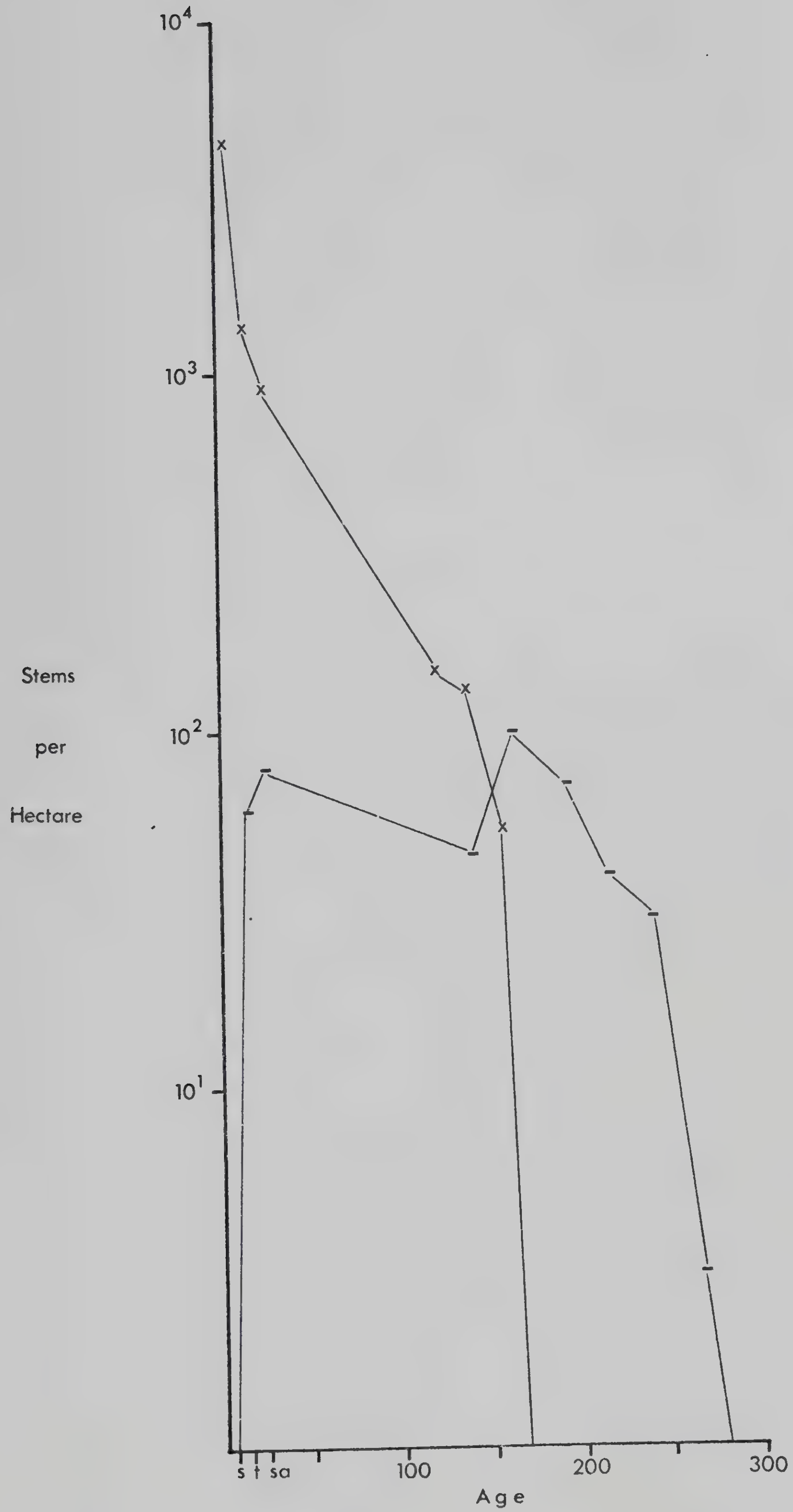
sites were quite moist.

Figures 19-22 show the age structure of the white spruce and balsam fir populations of a typical stand of each community type. Linear regression analyses predicting age from dbh (Figures 7 and 8) for each community type were used to establish an average age for the dbh size classes (10-20 cm, 20-30 cm, etc.) into which the trees were divided. The tree ages shown in the figures are age at breast height (1.35 m).

The seedling, transgressive, and sapling classes were plotted for all stands at 5, 15, and 50 years respectively on the basis of the average basal ages for these size classes. There was no significant difference either between spruce and fir (t test) or among the four community types (analysis of variance) in each of the three size classes.

The age structure patterns of spruce and fir in the four community types are similar. Of the two species, spruce becomes established first, followed by fir somewhat later. At present both species are reproducing with fir regeneration greatly out-numbering that of spruce. Spruce regeneration may be episodic, as indicated by stands which lack seedlings but have transgressives and saplings. Episodic seedling establishment seems tied to climatic and seed crop fluctuations (Boe 1954, Rowe 1955, Waldron 1965, Zasada and Gregory 1969, Roe et al. 1970, Zasada and Viereck 1970). A trend toward larger amounts of fir as succession proceeds is indicated by the preponderance of fir regeneration and the higher cover values for fir in the older stands studied.

Figure 19. Spruce and fir population analysis. _Rubus pedatus_/_Ptilium_ community type (Stand 7). s = seedlings, t = transgressives, sa = saplings, - = _Picea glauca_, x = _Abies balsamea_.



Stems
per
Hectare
10^4
10^3
10^2
10^1
s t sa
100
200
300
Age

Figure 20. Spruce and fir population analysis. *Cornus-Linnaea* community type (Stand 28).
s = seedlings, t = transgressives, sa = saplings,
- = *Picea glauca*, x = *Abies balsamea*.

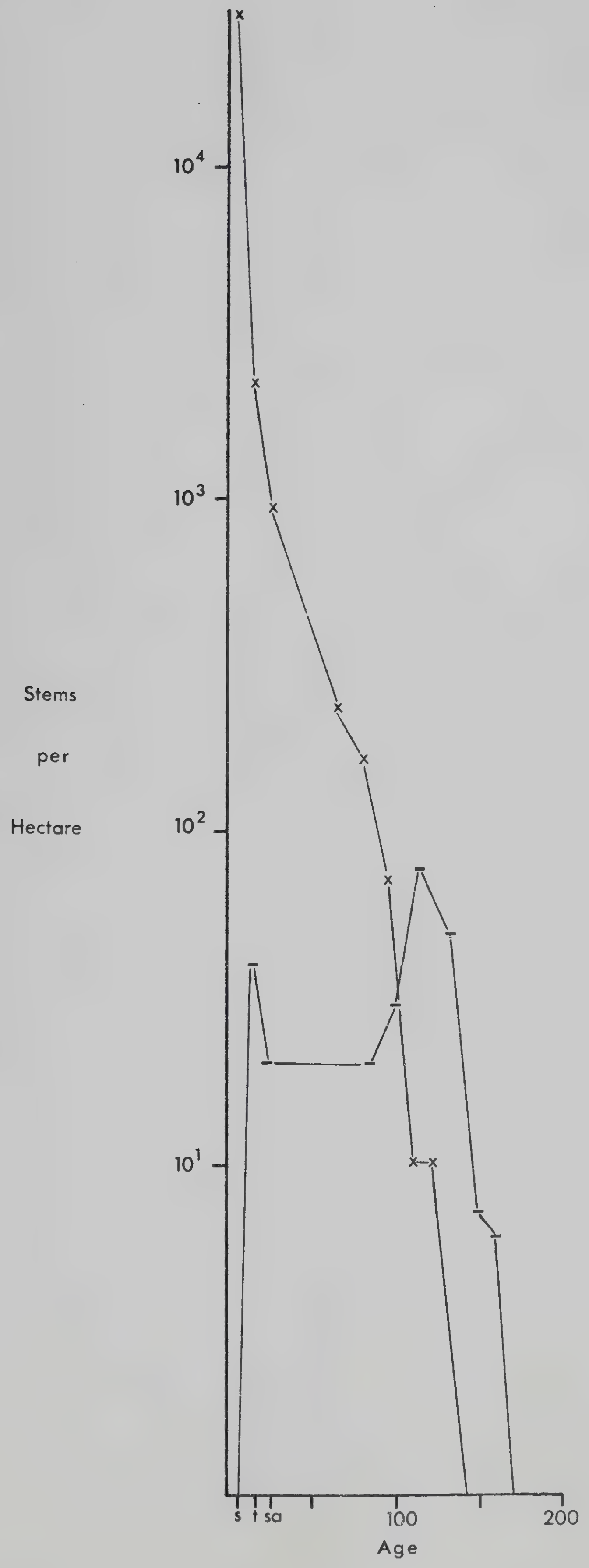
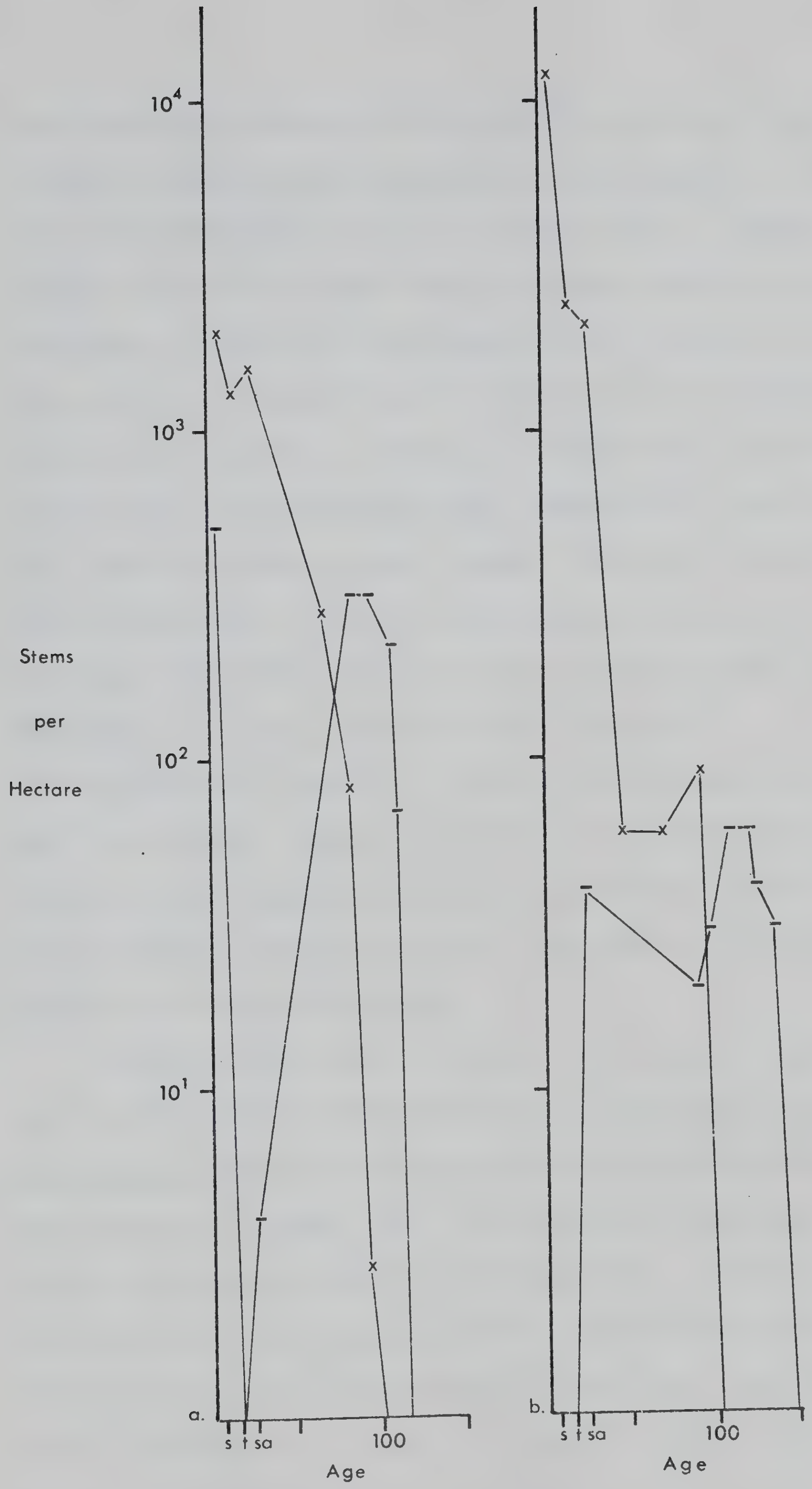

Stems
per
Hectare
10^4
10^3
10^2
10^1
s t sa
100
200
Age

Figure 21. Spruce and fir population analysis.
s = seedlings, t = transgressives, sa = saplings,
- = *Picea glauca*, x = *Abies balsamea*.

a. *Viburnum*/*Hylocomium* community type (Stand 17).

b. *Calamagrostis canadensis* community type (Stand 4).


Stems
per
Hectare
10^4
10^3
10^2
10^1
a.
s t sa
100
Age
b.
s t sa
100
Age

The latter point, however, is confounded by the oldest stands occurring at higher elevations where moisture conditions appear to be more favorable for fir (Rowe 1961, Bakuzis and Hansen 1965). Neither does abundant regeneration insure eventual canopy dominance, and quantitative information on the fate of the regeneration is lacking. As mentioned above, there is evidence that fir suffers a larger mortality and this, coupled with the shorter lifespan of fir (200 years, Horton 1956) as compared with spruce (300-350 years, Horton 1956), insures that spruce will remain in old-age stands. Whether the forest eventually becomes dominated by spruce or by fir probably depends on the local site conditions (Rowe 1961), with fir being favored at higher elevations and white spruce at lower elevations in the study area.

Whittaker has pointed out that the terms "climax" and "succession" refer "to different degrees of instability or of approach to a steady state no longer changing successionally" (Whittaker 1953). No other upland vegetation types in the study area appear to be as stable (long-lived) as the spruce-fir forests.

In summary, while there is lack of corroborative evidence from stands undisturbed for 350 years or more (longer than the lifespan of *Picea glauca*), there are two sources of evidence which indicate that these spruce-fir forests are a climax vegetation type, *i.e.* composed of self-perpetuating spruce and fir populations. The first is the evidence of self-regeneration shown by the population analyses. The second source is the lack of evidence of any other vegetation types or species capable or replacing them. There is evidence of increasing amounts of fir for the first 200 years or so, but the trend apparently

does not appear to continue to pure fir forest. This trend appears to be strongest at the higher elevations in the study area and weaker in the lower elevations.

SUMMARY

Thirty stands of spruce-fir forest in highland areas of northern Alberta were studied to provide: 1) a description and classification of these forests, and 2) a description of selected site characteristics.

The highlands are erosional remnants, underlain by flat-lying bedrock of late Cretaceous or Tertiary Age, which rise 300-600 m above the lowlands. The bedrock is capped usually with glacial till, but in some areas with unconsolidated, upper Tertiary gravels. Pleistocene ice left the area about 11,000 years BP.

During the growing season (May - September) the highlands are cooler and receive more precipitation than the adjacent lowlands.

Orthic Grey Luvisols were the most common soil type found. They occurred on all types of parent material on well to moderately well drained sites, and appear to be the most extensive soil type in upland sites under forest vegetation. Other soil types found were: Gleyed Grey Luvisol, both Orthic and Degraded Dystric Brunisols, Bisequa Humo-Ferric Podzol, and Orthic Regosol.

A Morphological Index evaluation of the spruce and fir species populations showed the spruce to be basically *Picea glauca* with varying amounts of introgression from *P. engelmannii* and the fir to be primarily *Abies balsamea* with some introgression from *A. lasiocarpa*. The pine populations were nearly all *Pinus contorta* var. *latifolia* with the easternmost stands studied showing intergradation with *P. banksiana*. A Geographic Index, based on the spruce, fir and pine populations, showed a trend of increasing "boreality" from west to east and from

high altitude to low altitude in the study area.

Using both ordination and cluster analysis four community types were recognized.

The Rubus pedatus/Ptilium community type had a nearly pure conifer tree layer usually dominated by fir. Diameter growth of spruce and fir was slowest and the stands were the oldest and floristically most Cordilleran. Bryoid cover was highest and total tree cover lowest. The stands occurred at the highest altitudes studied (1220-1295 m).

The Cornus-Linnaea community type was intermediate between the Rubus pedatus/Ptilium and Viburnum/Hylocomium community types in terms of floristic composition, position on the ordination field, and the geographic and altitudinal locations of the stands.

The Viburnum/Hylocomium community type was the most common type sampled (15 of 30 stands). The stands were generally mixedwood. Mean total tree cover, density, and basal area were highest. Mean total herb-dwarf shrub cover, mean stand age and mean stand altitude were lowest.

The Calamagrostis canadensis community type was characterized by Calamagrostis canadensis being dominant in the understory. Mean tree density, mean spruce and fir morphological index values, and mean total bryoid cover were lowest. Mean total herb-dwarf shrub cover was highest.

Simple correlation analysis and the plotting of non-vegetational variables on the ordination field revealed that both altitude and a group of six soil variables showed correlated trends across the ordination field. The altitudinal trend was interpreted as indicating

decreasingly favorable moisture conditions from the upper left of the field to the lower right. The soil variables showed a gradient from higher soil nutrient levels in the lower right of the field, to lower levels to the upper left.

Thus, the Rubus pedatus/Ptilium community type was associated with higher precipitation, cooler temperatures, and a lower soil nutrient status than the Viburnum/Hylocomium community type, which was conversely drier and warmer with richer soils. The other two community types were generally intermediate in both altitude and soil fertility values.

Community pattern was examined using correlation analysis and by plotting vegetational variables on the ordination field. Two groups of positively correlated variables were apparent, which were also correlated with the altitudinal and soil fertility gradients recognized.

The first group included: Abies balsamea cover, Pinus contorta cover, Ledum groenlandicum cover, Rubus pedatus cover, Vaccinium membranaceum cover, Ptilium crista-castrensis cover, Pleurozium schreberi cover, total bryoid cover, stand age, and both spruce and fir morphological index values. This group was associated with higher altitudes and lower soil fertility values and corresponded largely to the Rubus pedatus/Ptilium community type. The second group included: Picea glauca cover, Populus tremuloides cover, total tree cover, total tree density, Viburnum edule cover, Rosa acicularis cover, total shrub cover, Rubus pubescens cover, Linnaea borealis cover, and Hylocomium splendens cover. This second group was associated with lower altitudes and higher soil fertility levels and corresponded generally with the Viburnum/Hylocomium community type.

The flora of the study area was basically boreal but contained 12 plants of cordilleran or Pacific affinities. The Rubus pedatus/ Ptilium community type contained the largest number of "western" floristic elements, and the Viburnum/Hylocomium community type had the fewest.

Watt Mountain was identified as an additional outlier of the Lower Foothills Section (B19a). The Christina highland is best left in the Mixedwood Section (B18a).

Comparisons were made with studies of other workers in northern Alberta and regions adjacent to the study area. The Rubus pedatus/ Ptilium community type has its greatest affinity with the spruce-fir forests of the Far-Northern Rocky Mountains of Alberta, northern British Columbia and southwestern Northwest Territories. The Cornus-Linnaea community type shows closest relationships to the cordilleran forests of Alberta and northern British Columbia. The Viburnum/ Hylocomium community type is related most closely to the mixedwood forests of the closed boreal forest which extends from Alaska to Newfoundland. Forests similar to the Calamagrostis canadensis community type have been described from Alaska, and Manitoba and Saskatchewan.

Fire has had a marked impact on the western boreal forest and all of the stands investigated appeared to have originated following fire. The Rubus pedatus/Ptilium community type appears to have developed from pine-white spruce or pine-black spruce seral communities, the Cornus-Linnaea community type from pine-aspen-white spruce stages, and the Viburnum/Hylocomium and Calamagrostis canadensis community types pri-

marily from aspen-white spruce seral stages. The spruce-fir forests studied are considered to be a climax vegetation type based on evidence from analyses of the spruce and fir populations and on the absence of any other vegetation types or species which seem capable of replacing them. Balsam fir appears to be favored to become dominant at higher altitudes in the study area. With decreasing altitude the balance shifts to white spruce.

LITERATURE CITED

Anderson, E. 1949. Introgressive Hybridization. J. Wiley and Sons, Inc., New York.

Anderson, T.D. and A.R. Tiedemann. 1970. Periodic variation in physical and chemical properties of two central Washington soils. U.S. Dep. Agr. For. Serv. Res. Note PNW-125.

Austin, L. 1929. The Eddy tree breeding station. Madrono 1:203-213.

Baker, F.C. 1950. Principles of Silviculture. McGraw-Hill Book Comp. Inc., New York.

Bakuzis, E.V. and H.L. Hansen. 1965. Balsam fir: a monographic review. Univ. Minn. Press, Minneapolis.

Bayrock, L.A. 1959. Surface geology. Appendix _In_ J.D. Lindsay, _et al_. 1959.

__________. 1960. Surface geology. Appendix _In_ J.D. Lindsay, _et al_. 1960.

__________. 1963. Surficial geology. Appendix _In_ J.D. Lindsay, _et al_. 1963.

Beals, E. 1960. Forest bird communities in the Apostle Islands of Wisconsin. Wilson Bull. 72:156-181.

Beil, C.E. 1966. An ecological study of the primary producer level of the subalpine spruce-fir ecosystem of Banff and Jasper National Parks, Alberta. MSc thesis, Univ. Alberta, Edmonton.

Blake, I.H. 1945. An ecological reconnaissance in the Medicine Bow Mountains. Ecol. Monog. 15:207-247.

Bloomberg, W.J. 1950. Fire and spruce. For. Chron. 26:157-161.

Boe, K.N. 1954. Periodicity of cone crops for five Montana conifers. Proc. Mont. Acad. Sci. 14:5-9.

Boivin, B. 1959. _Abies balsamea_ (Linne) Miller et ses variations. Nat. Can. 86:219-223.

________. 1967. Flora of the Prairie Provinces. Phytologia 15:155.

Bouyoucos, G.T. 1951. A recalibration of the hydrometer method for making mechanical analysis of soils. Agron. J. 43:434-438.

Bray, J.R. and J.T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monog. 27:325-349.

Britton, D.M. 1972. Spinulose wood ferns Dryopteris in western North America. Can. Field-Nat. 86:241-247.

Canada Department of Agriculture. 1970. The system of soil classification for Canada. Queen's Printer, Ottawa.

Conway, P.W. 1972. Agglomerative hierarchical clustering with dendrograms. mimeo. Univ. Alberta Computing Services, Edmonton.

Cormack, R.G.H. 1953. A survey of coniferous succession in the eastern Rockies. For. Chron. 29:218-232.

Corns, I.G.W. 1972. Early plant succession after clearcutting of lodgepole pine forests in the Lower Foothills of Alberta. MSc thesis, Univ. Alberta, Edmonton.

Critchfield, W.G. and E.L. Little, Jr. 1966. The geographic distribution of the pines of the world. U.S. Dep. Agr. Misc. Publ. 991.

Cronquist, A., A.H. Holmgren, N.H. Holmgren and J.L. Reveal. 1972. Intermountain Flora. Vol. 1. Hafner Publ. Co., Inc. New York.

Daubenmire, R. 1943. Vegetational zonation in the Rocky Mountains. Bot. Rev. 9:326-393.

__________. 1959. A canopy-coverage method of vegetation analysis. Northw. Sci. 33:43-64.

__________. 1968. Some geographic variations of Picea sitchensis and their ecologic interpretation. Can. J. Bot. 46:787-798.

__________. 1970. Steppe vegetation of Washington. Wash. Agr. Exp. Sta. Tech. Bull. 62.

__________ and J.B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Wash. Agr. Exp. Sta. Tech. Bull. 60.

Day, R.J. 1972. Stand structure, succession and use of southern Alberta's Rocky Mountain forest. Ecology 53:472-478.

Despain, D.G. 1971. The vegetation of the Bighorn Mountains in relation to substrate and climate. PhD thesis, Univ. Alberta, Edmonton.

Dix, R.L. and J.M.A. Swan. 1971. The roles of disturbance and succession in upland forest at Candle Lake, Saskatchewan. Can. J. Bot. 49:657-676.

Dugle, J.R. 1966. A taxonomic study of western Canadian species in the genus Betula. Can. J. Bot. 44:929-1007.

Easton, J. and D. Precht. no date. Beals' ordination program. mimeo. Univ. Alberta Computing Services, Edmonton.

Garman, E.H. 1957. The occurrence of spruce in the interior of British Columbia. Brit. Col. For. Serv. Tech. Publ. T. 49.

Gauch, H.G., Jr. and R.H. Whittaker. 1972. Comparison of ordination techniques. Ecology 53:868-875.

Gersper, P.L. and N. Holowaychuk. 1961. Some effects of stem flow from forest canopy trees on chemical properties of soils. Ecology 52:691-702.

Gravenor, C.P. and L.A. Bayrock. 1961. Glacial deposits of Alberta. In Soils of Canada, ed. R.F. Legget. Royal Soc. Can. Spec. Publ. 3:33-50.

Green, R. and G.B. Mellon. 1962. Geology of the Chinchaga River and Clear Hills (north half) map areas, Alberta. Res. Council Alberta, Prelim. Rep. 62-8.

Habeck, J.R. 1965. A case of suspected introgressive hybridization between white, blue and Engelmann spruce in western Montana. Proc. Mont. Acad. Sci. 24:5 (Abstract).

__________. 1967. The vegetation of northwestern Montana: a preliminary report. Dep. Bot. Univ. Mont., Missoula.

__________ and T.W. Weaver. 1969. A chemosystematic analysis of some hybrid spruce (Picea) populations in Montana. Can. J. Bot. 47:1565-1570.

Hale, M.E., Jr. and W.L. Culberson. 1970. A fourth checklist of lichens of the continental United States and Canada. Bryol. 73:499-543.

Halliday, W.E.D. 1929. Forest types: Pasquia Forest Reserve. Unpubl. Rep., Can. Dep. Interior. In J.S. Rowe 1956.

__________. 1930. Rate of growth sruvey, Manitoba-Saskatchewan. Unpubl. Rep., Can. Dep. Interior. In J.S. Rowe 1956.

Hare, F.K. and J.C. Ritchie. 1972. The boreal bioclimates. Geogr. Rev. 62:333-365.

Harlow, W.M. and E.S. Harrar. 1958. Textbook of dendrology. McGraw-Hill, New York.

Heringa, P.K. and R.G.H. Cormack. 1963. The relation of soils and ground cover vegetation in even-aged pine stands of central Alberta. For. Chron. 39:273-278.

Horton, K.W. 1955. Early developments in a sub-alpine lodgepole pine stand of fire origin. Can. Dep. North. Affairs Nat. Resources, For. Res. Div. Tech. Note 16.

__________. 1956. The ecology of lodgepole pine in Alberta and its role in forest succession. Can. Dep. North. Affairs Nat. Resources, For. Res. Div. Tech. Note 45.

__________. 1959. Characteristics of subalpine spruce in Alberta. Can. Dep. North. Affairs Nat. Resources, For. Res. Div. Tech. Note 76.

Illingworth, K. and J.W.C. Arlidge. 1960. Interim report on some forest site types in lodgepole and spruce-alpine fir stands. Brit. Col. For. Serv. Res. Note 35.

Jeffrey, W.W. 1964. Forest types along lower Liard River, Northwest Territories. Can. Dep. For. Rural Dev., Dep. For. Publ. 1035.

Jones, J.F. 1962. Reconnaissance groundwater study Swan Hills and adjacent areas, Alberta. Res. Council Alberta, Prelim. Rep. 62 62-5.

__________. 1966. Geology and groundwater resources of the Peace River district, northwestern Alberta. Res. Council Alberta, Bull. 16.

Kirby, C.L. and R.T. Ogilvie. 1969. The forests of the Marmot Creek Watershed Research Basin. Dep. Fish. For., Can. For. Serv. Publ. 1259.

Kirkwood, J.E. 1922. Forest distribution in the northern Rocky Mountains. Univ. Mont. Bull. 247.

Klaehn, F.M. and J.A. Winieski. 1962. Interspecific hybridization in the genus Abies. Silvae Genet. 11:130-142.

Krajina, V.J. 1965. Biogeoclimatic zones and classification of British Columbia. In Ecology of Western North America, ed. V.J. Krajina, 1:1-17. Dep. Bot. Univ. Brit. Col, Vancouver.

Kuchar, P. 1973. Habitat types of Waterton Lakes National Park. Can. Dep. Indian Affairs North. Dev., Nat. Hist. Parks Br., Contract WR 54-72 Report.

Kujala, V. 1945. Waldvegetationsuntersuchungen in Kanada. Annales Acad. Sci. Fennicae, Ser. A, 4(7):1-426.

Langenheim, J.H. 1962. Vegetation and environmental patterns in the Crested Butte area, Gunnison County, Colorado. Ecol. Monog. 32:249-285.

La Roi, G.H. 1964. An ecological study of the boreal spruce-fir forests of the North American taiga. PhD thesis, Duke Univ., Durham, N.C.

__________. 1967. Ecological studies in the boreal spruce-fir forests of the North American taiga. I. Analysis of the vascular flora. Ecol. Monog. 37:229-253.

__________ and J.R. Dugle. 1968. A systematic and genecological study of Picea glauca and P. engelmannii, using paper chromatograms of needle extracts. Can. J. Bot. 46:649-687.

Lawton, E. 1971. Moss flora of the Pacific Northwest. J. Hattori Bot. Lab., Supplement 1.

Lesko, G.L. and J.D. Lindsay. 1973. Forest/soil relationships and management considerations in a portion of the Chip Lake map area, Alberta. Alberta Research, Edmonton. Rep. 73-1.

Lindsay, J.D., P.K. Heringa, S. Pawluk, and W. Odynsky. 1958. Exploratory soil survey of Alberta map sheets 84C (east half), 84B, 84A and 74D. Res. Council Alberta, Prelim. Soil Survey Rep. 58-1.

Lindsay, J.D., S. Pawluk, and W. Odynsky. 1959. Exploratory soil survey of Alberta map sheets 84D (north half), 84E, 84F and 84G. Res. Council Alberta, Prelim. Soil Survey Rep. 59-1.

Lindsay, J.D., S. Pawluk, and W. Odynsky. 1960. Exploratory soil survey of Alberta map sheets 84J, 84K and 84L. Res. Council Alberta, Prelim. Soil Survey Rep. 60-1.

Lindsay, J.D., S. Pawluk, and W. Odynsky. 1963. Exploratory soil survey of Alberta map sheets 74M, 74L, 74E and 73L (north half). Res. Council Alberta, Prelim. Soil Survey Rep. 63-1.

Lindsay, J.D., A. Wynnyk, and W. Odynsky. 1964. Exploratory soil survey of Alberta map sheets 83L, 83K, 83F and 83J. Res. Council Alberta, Prelim. Soil Survey Rep. 64-2.

Little, E.L., Jr. 1953. Checklist of the native and naturalized trees of the United States (including Alaska). U.S. Dep. Agr., Agr. Handbook 41.

Lutz, H.J. 1956. Ecological effects of forest fires in the interior of Alaska. U.S. Dep. Agr. Tech. Bull. 1133.

MacIver, D.C. 1970. Macroclimatic zonation in northern Alberta. MSc thesis, Univ. Alberta, Edmonton.

Mirov, N.T. 1956. Composition of turpentine of lodgepole X jack pine hybrids. Can. J. Bot. 34:343-357.

Moss, E.H. 1932. The vegetation of Alberta. IV. The poplar association and related vegetation of central Alberta. J. Ecol. 20:380-415.

__________. 1949. Natural pine hybrids in Alberta. Can. J. Res., C, 27:218-229.

__________. 1953. Forest communities in northwestern Alberta. Can. J. Bot. 31:212-252.

__________. 1955. The vegetation of Alberta. Bot. Rev. 21:493-567.

__________. 1959. Flora of Alberta. Univ. Toronto Press, Toronto.

__________ and G. Pegg. 1963. Noteworthy plant species and communities in westcentral Alberta. Can. J. Bot. 41:1079-1105.

Muttit, G.H. 1961. Spring and summer rainfall patterns in Alberta. Can. Dep. Transp., Met. Br. Circ. 3512, TEC 1961.

Newsome, R.D. and R.L. Dix. 1968. The forests of the Cypress Hills, Alberta and Saskatchewan, Canada. Amer. Midl. Nat. 80:118-185.

Odynsky, W., J.D. Lindsay, S.W. Reeder, and A. Wynnyk. 1961. Soil survey of the Beaverlodge and Blueberry Mountain sheets. Alberta Soil Survey Rep. 20.

Ogilvie, R.T. no date a. Ecology of vegetation in Banff National Park. mimeo. Dep. Biol. Univ. Calgary, Calgary.

__________. no date b. Spruce-fir habitat types of the Rocky Mountains north of Oldman River. mimeo. Dep. Biol. Univ. Calgary, Calgary.

__________. 1960. Spruce habitat types in the eastern slopes of the Rocky Mountains, Alberta. Unpubl. Rep. Can. Dep. North. Affairs Nat. Resources, For. Res. Div.

__________. 1962. Notes on plant distribution in the Rocky Mountains of Alberta. Can. J. Bot. 40:1091-1094.

__________. 1963. Ecology of the forests in the Rocky Mountains of Alberta. Can. Dep. For., For. Res. Br., Res. Rep. 63-A-12.

__________ and E. von Rudloff. 1968. Chemosystematic studies in the genus Picea (Pinaceae). IV. The introgression of white and Engelmann spruce as found along the Bow River. Can. J. Bot. 46:901-908.

Oosting, H.J. and J.F. Reed. 1952. Virgin spruce-fir forests in the Medicine Bow Mountains, Wyoming. Ecol. Monog. 22:69-91.

Patten, D.T. 1963. Vegetational pattern in relation to environments in the Madison Range, Montana. Ecol. Monog. 33:375-406.

Plochmann, R. 1956. Bestockungsaufbau und Baumartenwandel nordischer Urwalder. Beih. Forstwiss. Cbl. Forstwiss. Forsch. 6:1-96.

Poore, M.E.D. 1962. The method of successive approximation in descriptive ecology. Adv. Ecol. Res. 1:35-68.

Preston, R.J. 1961. North American trees. M.I.T. Press, Cambridge, Mass.

Pritchard, N.M. and A.J.B. Anderson. 1971. Observations on the use of cluster analysis in botany with an ecological example. J. Ecol. 59:727-747.

Raup, H.M. 1933. Notes on the distribution of white spruce and Banksian pine in northwestern Canada. J. Arnold Arbor. 14:335-344.

__________. 1934. Phytogeographic studies in the Peace and upper Liard River regions, Canada. Contr. Arnold Arbor. 6:1-111.

__________. 1946. Phytogeographic studies in the Athabasca-Great Slave Lake region. II. J. Arnold Arbor. 27:1-85.

__________. 1947. The botany of the southwestern Mackenzie. Sargentia 6:1-275.

Reeder, S.W. and W. Odynsky. 1965. Soil survey of the Cherry Point and Hines Creek area. Alberta Soil Survey Rep. 23.

__________. 1969. Soil survey of the Hotchkiss and Keg River Area. Alberta Soil Survey Rep. 26.

Revel, R.D. 1968. Phytocoenoses of the sub-boreal spruce zone. In National Res. Council Grant A-92 Progress Rep.:21-23, Dep. Bot. Univ. Brit. Col., Vancouver.

Righter, F.I. and P. Stockwell. 1949. The fertile species hybrid Pinus murraybanksiana. Madrono 10:65-69.

Roche, L. 1969. A genecological study of the genus Picea in British Columbia. New Phytol. 68:505-554.

Roe, A.L., R.R. Alexander, and M.D. Andrews. 1970. Engelmann spruce regeneration practices in the Rocky Mountains. U.S. Dep. Agr. For. Serv., Prod. Res. Rep. 115.

Rowe, J.S. 1955. Factors influencing white spruce reproduction in Manitoba and Saskatchewan. Can. Dep. North. Affairs Nat. Resources, For. Res. Div. Tech. Note 3.

__________. 1956. Vegetation of the southern boreal forest in Saskatchewan and Manitoba. PhD thesis, Univ. Manitoba, Winnipeg.

__________. 1959. Forest regions of Canada. Can. Dep. North. Affairs Nat. Resources, For. Br. Bull. 123.

__________. 1961. Critique of some vegetational concepts as applied to the forests of northwestern Alberta. Can. J. Bot. 39:1007-1017.

Sabbagh, M.E. and R.A. Bryson. 1962. An objective precipitation climatology of Canada. Univ. Wisc. Dep. Meteorol. Tech. Rep. 8.

Scheelar, M.D. and W. Odynsky. 1968. Soil survey of the Grimshaw and Notikewin area. Alberta Soil Survey Rep. 25.

Schofield, W.B. 1968. A checklist of Hepaticae and Anthocerotae of British Columbia. Syesis 1:157-162.

Scotter, G.W. 1963. Effects of forest fires on soil properties in northern Saskatchewan. For. Chron. 39:412-421.

Sørensen, T.A. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content, and its application to analyses of the vegetation of Danish commons. Biol. Skr. K. Danske Vidensk. Selsk. 5:1-34.

Stahelin, R. 1943. Factors influencing the natural restocking of high altitude burns by coniferous trees in the central Rocky Mountains. Ecology 24:19-30.

Stringer, P.W. and G.H. La Roi. 1970. The douglas fir forests of Banff and Jasper National Parks, Canada. Can. J. Bot. 48:1703-1726.

Sukachev, V. and N. Dylis. 1964. Fundamentals of forest biogeocoenology. (transl. J.M. Maclennan). Oliver and Boyd Ltd., London.

Swan, J.M.A. and R.L. Dix. 1966. The phytosociological structure of upland forest at Candle Lake, Saskatchewan. J. Ecol. 54:13-40.

Taylor, T.M.C. 1959. The taxonomic relationship between Picea glauca (Moench) Voss and P. engelmannii Parry. Madrono 15:111-115.

van Groenewoud, H. 1965a. An analysis and classification of white spruce communities in relation to certain habitat features. Can. J. Bot. 43:1025-1036.

__________. 1965b. Ordination and classification of Swiss and Canadian coniferous forests by various biometric and other means. Ber. Geobot. Inst. ETH Stiftg. Rubel, Zurich 36:28-102.

Weaver, T.W. 1965. Variation in the spruce complex of the northern Rocky Mountains: *Picea glauca*, *P. pungens* and *P. engelmannii*. MA thesis, Univ. Mont., Missoula.

Waldron, R.M. 1965. Cone production and seedfall in a mature white spruce stand. For. Chron. 41:314-329.

Whittaker, R.H. 1953. A consideration of climax theory: the climax as a population and pattern. Ecol. Monog. 23:41-78.

__________. 1956. Vegetation of the Great Smoky Mountains. Ecol. Monog. 26:1-80.

__________. 1967. Gradient analysis of vegetation. Biol. Rev. 42:207-264.

Wright, J.W. 1955. Species crossability in spruce in relation to distribution and taxonomy. For. Sci. 1:319-349.

Wynnyk, A., J.D. Lindsay, P.K. Heringa, and W. Odynsky. 1964. Exploratory soil survey of Alberta map sheets 83O, 83P, and 73M. Res. Council Alberta, Prelim. Soil Survey Rep. 64-1.

Wynnyk, A., J.D. Lindsay, and W. Odynsky. 1969. Soil survey of the Whitecourt and Barrhead area. Alberta Soil Survey Rep. 27.

Zasada, J.C. and R.A. Gregory. 1969. Regeneration of white spruce with reference to interior Alaska: a literature review. U.S. Dep. Agr. For. Serv., Res. Paper PNW-79.

Zasada, J.C. and L.A. Viereck. 1970. White spruce cone and seed production in interior Alaska. U.S. Dep. Agr. For. Serv., Res. Note PNW-129.

Zavarin, E. and K. Snajberk. 1965. Chemotaxonomy of the genus *Abies*. I. Survey of the terpenes present in the *Abies* balsams. Phytochem. 4:141-148.

__________. 1972. Geographic variability of monoterpenes from *Abies balsamea* and *A. fraseri*. Phytochem. 11:1407-1421.

Zavarin, E., W.B. Critchfield, and K. Snajberk. 1969. Turpine composition of *Pinus contorta* X *Pinus banksiana* hybrids and hybrid derivatives. Can. J. Bot. 47:1443-1453.

Zavarin, E., K. Snajberk, T. Reichert, and E. Tsien. 1970. On the geographic variability of the monoterpenes from the cortical blister oleoresin of *Abies lasiocarpa*. Phytochem. 9:377-396.

Zinke, P.J. 1962. The pattern of influence of individual forest trees on soil properties. Ecology 43:130-133.

Appendix I. Soil profile characteristics. S = sand, Si = silt, C = clay, L = loam, HC = heavy clay, ASW = available soil water, TEC = total exchange capacity. See text for methodological details.

Horizon	Thickness (cm)	pH	Particle Size			Texture	ASW (%)	Exchangeable Cations (meq/100 g)				
			%S	%Si	%C			TEC	Ca^{++}	Mg^{++}	K^{+}	Na^{+}
Stand 1 - Orthic Grey Luvisol												
L-H	8	5.5	--	--	--	--	--	55.4	49.4	4.2	1.2	0.1
Ah	4	4.6	52	27	21	SCL	16.4	23.6	14.1	2.2	1.9	0.1
Ae	6	3.8	40	31	29	CL	14.0	22.6	8.8	1.4	0.3	0.1
Bt	35	3.6	30	28	42	C	16.3	34.2	15.9	3.3	0.5	0.2
C	--	3.7	31	27	42	C	18.4	23.1	17.5	2.8	0.5	0.4
Stand 2 - Orthic Grey Luvisol												
L-H	5	4.9	--	--	--	--	--	58.3	50.0	4.1	2.4	0.1
Ae	15	4.1	47	34	19	L	15.1	5.7	2.2	0.8	0.2	0.2
Bt	20	4.0	38	29	33	CL	14.6	12.3	5.6	1.8	0.2	0.5
C	--	3.2	22	19	59	C	16.9	39.9	18.8	6.7	0.9	0.4
Stand 3 - Orthic Grey Luvisol												
L-H	8	6.0	--	--	--	--	--	83.7	75.0	5.3	2.6	0.7
Ae	10	5.0	46	43	11	L	12.7	13.7	10.2	1.0	0.2	0.0
Bt	46	5.5	49	22	29	SCL	12.3	18.2	14.6	2.8	0.3	0.1
C	--	4.9	39	28	33	CL	13.5	18.6	14.7	3.1	0.4	0.2

Appendix I - Continued

Horizon	Thickness (cm)	pH	Particle Size %S	%Si	%C	Texture	ASW (%)	Exchangeable Cations (meq/100 g) TEC	Ca^{++}	Mg^{++}	K^{+}	Na^{+}
Stand 4 - Orthic Grey Luvisol												
L-H	6	4.1	--	--	--	--	--	72.6	10.2	2.8	2.6	0.1
Ae	10	3.6	50	34	16	L	17.8	9.2	3.3	0.4	0.3	0.0
Bt	20	4.6	44	30	26	L	16.2	22.4	44.1	0.8	0.2	0.1
C	--	4.6	49	20	31	SCL	14.1	12.9	6.7	1.8	0.3	0.2
Stand 5 - Orthic Grey Luvisol												
L-H	5	4.4	--	--	--	--	--	41.6	27.0	4.1	2.3	0.6
Ahej	6	3.7	28	50	22	L	20.8	15.1	7.8	1.2	0.4	0.3
Bt	26	4.1	27	43	30	CL	15.4	19.0	10.3	2.5	0.4	0.3
C	--	4.2	20	20	60	C	17.6	29.2	20.0	5.3	0.3	0.1
Stand 6 - Orthic Grey Luvisol												
L-H	8	3.3	--	--	--	--	--	40.7	14.0	2.8	2.6	0.7
Ae	10	3.5	20	55	25	SiL	26.4	7.2	11.6	0.5	0.3	0.1
Bt	42	4.6	16	36	48	C	19.6	11.3	2.8	1.2	0.3	0.1
C	--	4.3	27	48	25	L	20.4	26.2	13.5	3.7	0.5	0.2

Appendix I - Continued

Horizon	Thickness (cm)	pH	Particle Size %S	%Si	%C	Texture	ASW (%)	Exchangeable Cations (meq/100g) TEC	Ca^{++}	Mg^{++}	K^{+}	Na^{+}
Stand 7 - Orthic Grey Luvisol												
L-H	7	3.7	--	--	--	--	--	31.3	10.5	3.7	2.9	1.2
Ae	12	3.6	30	46	24	L	21.5	16.6	2.9	0.6	0.5	0.2
Bt	33	4.5	16	41	43	SiC	26.9	8.1	5.0	2.1	0.5	0.2
C	--	4.2	18	35	47	C	26.3	14.0	9.7	3.3	0.1	0.4
Stand 8 - Orthic Dystric Brunisol												
L-H	9	3.7	--	--	--	--	--	45.7	27.0	5.3	2.7	0.2
Aej	10	3.8	48	29	23	L	23.5	6.1	3.5	1.1	0.5	0.1
Bm	31	4.2	49	29	22	L	20.5	5.9	4.6	1.6	0.3	0.5
C	--	4.0	40	30	30	CL	19.7	14.3	7.5	2.3	0.5	0.1
Stand 9 - Degraded Dystric Brunisol												
L-H	8	3.6	--	--	--	--	--	48.3	19.5	2.5	2.9	0.5
Ae	10	3.7	25	53	22	SiL	29.6	13.6	3.5	0.8	0.5	0.1
Btfj	25	4.6	27	49	24	SiL	19.5	9.7	3.8	2.5	0.4	0.1
C	--	4.7	34	23	43	C	14.2	27.4	16.3	3.0	0.5	0.2
Stand 10 - Bisequa Humo-Ferric Podzol												
L-H	10	3.6	--	--	--	--	--	18.1	11.0	3.3	2.2	0.2
Ae	20	3.4	24	53	23	SiL	22.4	12.8	2.3	0.8	0.2	0.1
Bf	18	4.5	35	37	28	CL	20.8	8.7	33.0	1.0	0.2	0.1
Bt	25	4.4	31	36	33	CL	17.0	16.3	12.0	1.6	0.4	0.2
IIC	--	4.9	63	18	19	SL	10.1	5.3	2.2	1.8	0.2	0.1

Appendix I - Continued

Horizon	Thickness (cm)	pH	Particle Size %S	Particle Size %Si	Particle Size %C	Texture	ASW (%)	Exchangeable Cations (meq/100 g) TEC	Ca^{++}	Mg^{++}	K^{+}	Na^{+}
Stand 11 - Orthic Grey Luvisol												
L-H	5	4.9	--	--	--	--	--	62.6	56.3	3.3	2.2	0.6
Ae	8	3.4	30	46	24	L	21.8	14.2	4.0	1.7	0.4	0.2
Bt	28	4.4	34	25	41	C	10.9	18.1	14.2	2.1	0.5	0.3
C	--	4.7	34	23	43	C	14.2	27.4	16.3	3.0	0.5	0.2
Stand 12 - Orthic Grey Luvisol												
L-H	10	4.6	--	--	--	--	--	60.8	46.9	2.6	1.9	1.0
Ae	10	4.5	39	42	19	L	20.6	9.0	5.2	0.8	0.4	0.1
Bt	23	4.1	35	27	38	CL	17.5	23.4	14.4	1.6	0.3	0.1
C	--	4.1	37	26	37	CL	17.1	21.0	15.3	3.3	0.6	0.2
Stand 13 - Orthic Dystric Brunisol												
L-H	4	5.1	--	--	--	--	--	62.9	50.0	3.6	2.4	0.1
Ah	4	4.9	49	34	17	L	16.5	9.2	8.9	1.0	0.7	0.1
Bm	30	5.1	67	16	17	SL	12.2	11.1	9.4	2.6	0.3	0.1
C	--	4.0	28	36	36	CL	24.1	23.2	17.9	3.6	0.6	0.2
Stand 14 - Orthic Grey Luvisol												
L-H	9	4.4	--	--	--	--	--	51.3	43.1	5.1	0.1	0.2
Ae	13	4.2	27	50	23	SiL	19.0	14.9	7.3	1.5	0.5	0.1
Bt	35	4.7	24	47	29	CL	17.7	15.6	7.0	1.7	0.3	0.1
C	--	4.3	31	21	48	C	20.2	32.9	22.7	3.8	1.0	0.2

Appendix I - Continued

Horizon	Thickness (cm)	pH	Particle Size %S	%Si	%C	Texture	ASW (%)	Exchangeable Cations (meq/100 g) TEC	Ca^{++}	Mg^{++}	K^{+}	Na^{+}
Stand 15 - Orthic Grey Luvisol												
L-H	7	5.6	--	--	--	--	--	95.8	81.2	4.7	8.6	0.5
Ae	10	4.5	42	30	28	CL	18.0	8.9	4.7	0.7	0.4	0.1
Bt	21	3.6	42	19	39	CL	15.3	12.8	11.3	0.9	0.4	0.2
C	--	3.9	45	23	33	SCL	14.5	16.9	6.9	2.1	0.3	0.4
Stand 16 - Orthic Grey Luvisol												
L-H	5	5.0	--	--	--	--	--	97.7	82.5	6.6	1.4	0.5
Ae	8	3.5	59	28	13	SL	9.4	3.1	1.8	0.6	0.3	0.2
Bt	30	4.5	60	20	20	SCL	9.7	3.9	3.5	0.4	0.3	0.1
C	--	5.2	35	24	41	C	11.2	17.7	15.5	1.2	0.5	0.2
Stand 17 - Orthic Grey Luvisol												
L-H	9	5.1	--	--	--	--	--	93.4	80.0	7.7	2.1	0.1
Ae	8	5.2	24	49	27	CL	25.3	43.4	11.3	5.1	1.5	0.1
Bt	18	4.8	15	41	44	C	24.6	47.5	35.0	4.1	1.3	0.1
C	--	4.9	31	37	32	CL	22.6	29.3	22.5	3.6	0.5	0.2
Stand 18 - Orthic Grey Luvisol												
L-H	8	4.6	--	--	--	--	--	53.6	38.8	3.6	1.8	0.4
Ah	5	4.3	46	38	16	L	22.8	14.9	5.5	0.7	0.3	0.3
Ae	8	4.1	48	35	17	L	14.9	8.1	4.3	0.5	0.1	0.1
Bt	20	4.2	47	27	26	L	14.0	14.4	7.7	1.8	0.2	0.1
C	--	5.0	48	32	20	L	17.9	31.8	20.3	6.3	1.2	0.1

Appendix I - Continued

Horizon	Thickness (cm)	pH	Particle Size %S	%Si	%C	Texture	ASW (%)	Exchangeable Cations (meq/100 g) TEC	Ca^{++}	Mg^{++}	K^{+}	Na^{+}
Stand 19 - Orthic Grey Luvisol												
L-H	6	5.2	--	--	--	--	--	56.8	40.0	4.2	2.3	0.3
Ae	10	5.0	40	40	20	L	15.8	7.5	5.2	1.6	0.2	0.1
Bt	38	5.0	36	24	40	C	13.1	18.4	15.1	2.8	0.5	0.1
C	--	5.3	35	20	45	C	15.1	20.1	19.0	3.9	0.4	0.3
Stand 20 - Orthic Regosol												
L-H	5	4.6	--	--	--	--	--	36.9	18.0	3.3	2.1	0.6
Ah	6	4.6	63	22	15	SL	12.6	12.3	3.5	0.8	0.4	0.1
C	--	4.6	25	22	53	C	16.8	20.1	16.1	3.7	0.6	0.1
Stand 21 - Orthic Grey Luvisol												
L-H	6	5.1	--	--	--	--	--	52.9	49.0	5.3	2.9	0.6
Ae	10	4.8	28	39	33	CL	14.3	18.1	14.0	3.1	0.3	0.3
Bt	35	5.5	28	31	41	C	15.9	23.4	17.8	3.1	0.3	0.4
Ck	--	7.2	25	40	35	CL	30.1	43.4	32.5	4.3	0.4	0.2
Stand 22 - Gleyed Grey Luvisol												
L-H	8	5.8	--	--	--	--	--	99.8	80.0	16.0	2.7	0.6
Aegj	10	5.4	43	42	15	L	35.5	32.7	26.2	5.1	0.4	0.2
Btgj	25	7.1	35	32	33	CL	15.7	35.8	22.5	5.7	0.4	0.3
Ck	--	7.2	35	35	30	CL	18.8	40.0	26.9	4.9	0.4	0.5

Appendix I - Continued

Horizon	Thickness (cm)	pH	Particle Size %S	%Si	%C	Texture	ASW (%)	Exchangeable Cations (meq/100 g) TEC	Ca^{++}	Mg^{++}	K^{+}	Na^{+}
Stand 23 - Orthic Grey Luvisol												
L-H	7	5.9	--	--	--	--	--	72.6	57.7	4.9	3.1	0.6
Ae	10	4.3	21	43	36	CL	15.7	11.3	9.0	2.3	0.3	0.1
Bt	23	4.8	19	26	55	C	14.8	23.7	19.0	3.6	0.5	0.3
C	--	5.0	18	21	61	HC	14.6	37.3	23.0	5.9	0.5	0.4
Stand 24 - Degraded Dystric Brunisol												
L-H	8	5.5	--	--	--	--	--	98.3	85.0	9.8	2.6	0.9
Ae	12	4.6	25	34	41	C	17.8	24.7	14.4	4.7	1.0	0.2
Btj	30	5.1	17	34	49	C	19.6	25.8	19.3	5.7	1.2	0.3
C	--	5.2	10	34	56	C	17.5	19.2	14.6	7.2	1.8	0.8
Stand 25 - Orthic Grey Luvisol												
L-H	10	4.1	--	--	--	--	--	30.8	19.0	2.1	1.1	0.5
Ae	5	4.2	39	38	23	L	23.0	18.9	6.1	1.2	0.3	0.1
Bt	20	4.3	21	34	45	C	16.5	35.8	5.6	1.2	0.4	0.1
C	--	4.1	22	32	46	C	16.1	38.0	6.8	2.3	0.4	0.1
Stand 26 - Orthic Grey Luvisol												
L-H	8	4.4	--	--	--	--	--	51.1	27.8	6.9	2.2	0.5
Ae	8	3.4	30	40	30	CL	27.7	12.4	5.6	2.8	1.1	0.1
Bt	35	3.5	14	52	34	SiCL	29.2	22.5	8.8	2.4	1.0	0.3
C	--	3.8	37	30	33	CL	10.6	26.9	9.5	2.4	1.0	0.3

Appendix I - Continued

Horizon	Thickness (cm)	pH	Particle Size %S	Particle Size %Si	Particle Size %C	Texture	ASW (%)	Exchangeable Cations (meq/100 g) TEC	Ca^{++}	Mg^{++}	K^{+}	Na^{+}
Stand 27 - Orthic Dystric Brunisol												
L-H	7	3.2	--	--	--	--	--	48.8	14.0	2.1	1.1	0.3
Aej	6	4.2	25	42	33	CL	24.5	15.3	7.8	1.3	0.6	0.1
Bm	20	4.4	21	50	29	CL	23.6	26.6	10.3	2.1	0.5	0.3
C	--	5.3	27	24	49	C	23.9	35.2	32.5	2.6	1.0	0.4
Stand 28 - Orthic Grey Luvisol												
L-H	5	4.2	--	--	--	--	--	63.0	21.3	4.1	4.0	0.6
Ae	10	4.0	34	42	24	L	20.7	11.8	5.0	1.9	0.5	0.2
Bt	35	4.4	37	30	33	CL	15.1	29.0	9.0	2.1	0.4	0.1
C	--	4.7	24	25	51	C	18.9	23.0	17.1	3.7	1.1	0.3
Stand 29 - Bisequa Humo-Ferric Podzol												
L-H	6	3.6	--	--	--	--	--	35.6	11.3	3.3	0.5	0.6
Ae	15	3.8	36	35	29	CL	10.5	3.5	1.7	0.6	0.3	0.2
Bf	30	4.0	44	29	27	L	21.2	5.4	1.1	0.5	0.3	0.1
Btfj	35	4.4	55	10	35	SC	13.6	8.8	2.3	0.5	0.2	0.2
C	--	4.2	34	42	24	L	18.8	9.2	1.8	0.4	0.3	0.1
Stand 30 - Gleyed Grey Luvisol												
L-H	8	5.2	--	--	--	--	--	85.2	78.4	4.6	2.7	0.5
Aegj	10	6.2	26	42	32	CL	21.9	20.4	16.8	2.6	0.5	0.3
Btgj	25	6.6	34	21	45	C	13.9	34.3	26.7	3.9	1.0	0.2
Ck	--	6.8	32	22	46	C	17.1	38.1	30.4	4.1	1.1	0.2

Appendix II. Mean species cover by stand and community type for species not in Table 9. t = < 1% cover, + = present.

SPECIES	COMMUNITY TYPE AND STAND																													
	Rubus pedatus/ Ptilium						Cornus-Linnaea					Viburnum/Hylocomium															Calamagrostis canadensis			
	8	9	6	10	7	29	11	28	25	15	18	2	20	12	13	27	30	3	24	22	19	14	16	17	21	23	1	4	26	5
Shrub Layer																														
Betula glandulosa	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Picea mariana saplings	-	-	3	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ribes glandulosum	-	-	-	-	1	-	-	-	t	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sambucus pubens	-	-	-	-	t	-	1	3	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Populus tremuloides saplings	-	-	-	-	-	-	-	-	-	-	-	t	-	1	t	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
Lonicera dioica var. glaucescens	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-
Salix discolor	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ribes triste	-	-	-	-	-	-	-	-	-	-	-	-	-	t	t	-	-	-	-	-	-	-	-	t	-	-	-	1	-	-
Populus balsamifera transgressives	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	t	t	-	-	-	-	-	-
Betula papyrifera transgressives	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	t	-	-	-	-	-	t	-	-	-	-	-	-
Betula papyrifera saplings	-	-	-	-	-	-	-	-	-	-	-	-	-	1	t	-	-	-	-	-	-	1	-	-	-	-	-	-	t	-
Betula Xutahensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-
Symphoricarpos albus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	t	-	-	-	-	-	-
Alnus tenuifolia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	t	-	-	-	-	-	-	-
Populus balsamifera saplings	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	t	-	-	-	-	-	-
Cornus stolonifera	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-
Herb-Dwarf Shrub Layer																														
Gaultheria hispidula	-	t	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Arctostaphylos uva-ursi	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sorbus scopulina	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-
Lonicera involucrata	-	-	-	-	-	-	t	-	-	-	-	-	-	-	t	-	-	-	3	-	t	-	-	-	-	-	-	-	-	-
Urtica dioica	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Adoxa moschatellina	-	-	-	-	-	-	-	2	-	t	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	t	2	-
Osmorhiza depauperata	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	t	-	-	-	-	t	-	-	-	-	-	-	-	-
Arenaria lateriflora	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Heracleum lanatum	-	-	-	-	-	-	-	-	-	t	1	-	-	-	-	1	-	-	-	-	-	t	-	-	-	-	-	-	-	t
Lycopodium tristachyum	-	-	-	-	-	-	-	-	-	1	-	-	2	1	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-
Ribes oxyacanthoides	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	2	-	-	t	-	-	-	-	-	-	-	-
Aster conspicuus	-	-	-	-	-	-	-	-	-	-	t	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Populus tremuloides seedlings	-	-	-	-	-	-	-	-	-	-	t	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Elymus innovatus	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	t	-	-	-	-	1	t	-	-	-	-	-	-

Appendix II - Continued

	COMMUNITY TYPE AND STAND																													
	Rubus pedatus/ Ptilium						Cornus- Linnaea					Viburnum/Hylocomium															Calamagrostis canadensis			
SPECIES	8	9	6	10	7	29	11	28	25	15	18	2	20	12	13	27	30	3	24	22	19	14	16	17	21	23	1	4	26	5
SPECIES	8	9	6	10	7	29	11	28	25	15	18	2	20	12	13	27	30	3	24	22	19	14	16	17	21	23	1	4	26	5
H - D S Layer (cont.)																														
Geocaulon lividum	-	-	-	-	-	-	-	-	-	-	-	t	2	-	-	-	-	-	-	2	1	-	-	-	-	1	-	-	-	-
Poa palustris	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Calypso bulbosa	-	-	-	-	-	-	-	-	-	-	-	-	1	-	t	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-
Coptis trifolia	-	-	-	-	-	-	-	-	-	-	-	-	-	2	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t
Thalictrum sparsiflorum	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	t	-	-	-	-	t	-	-	-	-	-	-
Corallorhiza trifida	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Achillea millefolium	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	t	t	-	-	-	-	-	t	-	t	-	-	-	-
Delphinium glaucum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	t	-	t	-	-	-	-	1	-	-	-	-	-	-
Equisetum scirpoides	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	t	-	-	-	-	-	-	-	-	-	-	-	-	-
Habenaria obtusata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	t	t	t	-	-	-	-	-	-	-	-
Carex disperma	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-
Smilacina racemosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	2
Pyrola minor	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-
Ribes hirtellum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	t	-	-	-	-	-	-
Vicia americana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	t	-	-	-	-	-	-	-	-	-	-	-
Symphoricarpos albus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-
Amelanchier alnifolia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-
Lonicera dioica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-
Geum macrophyllum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-
Rubus acaulis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-
Impatiens capensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
Populus balsamifera seedlings	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-
Lilium philadelphicum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t
Stellaria calycantha	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t
Bryoid Layer																														
Polytrichum piliferum	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cetraria nivalis	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cetraria ericetorum	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cladonia phyllophora	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cladonia cornuta	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cladina alpestris	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Stereocaulon tomentosum	-	-	-	t	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cladonia fimbriata	-	-	-	t	-	-	-	-	-	-	-	-	-	t	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-
Cladina mitis	-	-	t	t	-	-	-	-	-	-	-	-	1	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lophozia adscendens	-	t	-	-	-	-	-	-	-	-	t	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sphagnum capillaceum	-	-	t	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dicranum flagellare	-	t	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tetraphis pellucida	-	t	t	-	-	t	-	-	-	t	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhytidiadelphus triquetris	-	-	-	-	-	t	-	-	-	-	-	t	-	-	-	-	t	-	-	-	t	-	t	-	-	-	-	-	-	-

Appendix II - Continued

SPECIES	COMMUNITY TYPE AND STAND																													
	Rubus pedatus/ Ptilium						Cornus-Linnaea					Viburnum/Hylocomium															Calamagrostis canadensis			
	8	9	6	10	7	29	11	28	25	15	18	2	20	12	13	27	30	3	24	22	19	14	16	17	21	23	1	4	26	5
Bryoid Layer (cont.)																														
Cladonia gracilis	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	t	-	-	-	-
Plagiomnium ciliare	-	-	-	-	t	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-
Cladonia chlorophaea	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sphagnum squarrosum	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brachythecium velutinum	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Plagiomnium rugicum	-	-	-	-	-	-	3	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Isopterygium elegans	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dicranum undulatum	-	-	-	-	-	-	-	-	-	t	t	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-
Cladonia multiformis	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	t	-	-	-	t	t	-	-	-	-
Oncophorus wahlenbergii	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	t
Tritomaria exsectiformis	-	-	-	-	-	-	-	-	t	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-
Brachythecium starkei	-	-	-	-	-	-	-	-	-	-	t	t	-	-	-	-	-	-	-	-	t	-	-	-	-	-	t	-	-	-
Lophocolea heterophylla	-	-	-	-	-	-	-	-	-	-	t	t	-	-	-	-	-	-	-	-	-	-	t	t	-	-	-	-	-	-
Jamesoniella autumnalis	-	-	-	-	-	-	-	-	-	t	t	-	-	-	-	-	-	-	-	-	-	-	t	t	-	t	-	-	-	-
Peltigera canina	-	-	-	-	-	-	-	-	-	-	-	t	t	-	-	-	-	-	-	-	-	-	t	t	-	t	-	-	-	-
Isopterygium pulchellum	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dicranum pallidisetum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lobaria pulmonaria	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Plagiomnium rostratum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Peltigera polydactyla	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-
Campylium hispidulum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-
Amblystegium serpens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-
Pseudoleskeela nervosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-
Cladina arbuscula	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	t	-	-	-	-	-
Plagiomnium orthorrhynchum	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cladonia cenotea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	t	-	-	-
Epiphytes																														
Alectoria sarmentosa	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hypogymnia tubulosa	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Usnea dasypoga	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Physcia adscendens	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Alectoria pseudofuscescens	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Usnea cavernosa	-	-	+	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nephroma resupinatum	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ramalina minuscula	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Usnea glabrescens	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Orthotrichum obtusum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Usnea scabiosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Parmelia septentrionalis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
Anaptychia speciosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-
Parmelia exasperatula	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-

SPECIAL COLLECTIONS

UNIVERSITY OF ALBERTA LIBRARY

REQUEST FOR DUPLICATION

I wish a photocopy of the thesis by

Spruce-Fir Forests of Northern Alberta (author)

entitled P.L. Achuff

The copy is for the sole purpose of private scholarly or scientific study and research. I will not reproduce, sell or distribute the copy I request, and I will not copy any substantial part of it in my own work without permission of the copyright owner. I understand that the Library performs the service of copying at my request, and I assume all copyright responsibility for the item requested.

Date	Name and address	Pages copied	Signature
Aug. 29/77	Edward Karpuk Box 174, Tomahawk Alberta	iv, 1, 3, 5, 6.	
Nov. 7/77	Richard Kabzems 211-11 Fairway Dr.	Title page, p. iv-ix, p. 1-6, 107-112, 121-135	Richard Kabzems

F. 236

September 1975